Humpback whale migration: new insights into the energetics of a long-distance migrant

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“The journey of a thousand miles begins with one step”

Lao Tzu

Declaration of Originality

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To my parents

Abstract

Knowledge of animal energetics is fundamental to the understanding of long distance migration and the strategies required for survival and reproduction during extensive journeys away from foraging areas. Baleen whales are ideal for such an investigation as their large body size allows huge energy stores and facilitates one of the longest migrations of all mammals. However, this large body size also prohibits their capture for measurement, making data collection extremely difficult. In this study I used a range of techniques to examine cetacean energy stores in order to improve our understanding of the energetics of the annual long-distance migration of humpback whales between high latitude feeding grounds and low latitude breeding grounds.

Specifically, I aimed to (1) ascertain the different energy store requirements of a capital breeding cetacean compared to those of an income breeding cetacean; (2) investigate how lactating female humpback whales manage their energy stores to maximise the growth of their dependent calves; (3) identify the extent of the Breeding Stock D (BSD) humpback whale calving grounds and discuss the energetic implications of an extended calving range.

I used a unique set of historical whaling records that detailed total body lipid to quantify the energy stores of two large cetacean species, the income breeding sperm whale (*Physeter macrocephalus*) and the capital breeding humpback whale (*Megaptera novaeangliae*). The relationships I quantified between body length and total body lipid demonstrated that cetacean energy stores vary according to body *size*, life history strategy, and reproductive class. More specifically, the capital breeding humpback whale stored 31.9 - 74.9% more energy to fuel the costs of their long-distance migration than the income breeding sperm whale; and pregnant female humpback whales stored 26.2% and 37.4% more energy than

non-pregnant females and males, respectively, to satisfy the high energy demands of lactation. The pregnant females that arrived in the breeding grounds later, presumably those that remained in the foraging grounds for longer durations, had larger energy stores than those that departed earlier. The findings highlighted that smaller (shorter) individuals, with their relatively small energy stores, and relatively high metabolic rates, experience higher levels of energetic stress during the migratory fast. This is particularly important for small juveniles and maternal females as they have high energy costs and relatively small endogenous energy reserves. In addition to providing information about cetacean energy stores that can be used in ecosystem and bioenergetics models, this study has provided a baseline of humpback whale body condition from the last century that can be used for comparison in the current era.

To extend the findings from the historical whaling era, I used aerial photogrammetric techniques on free-swimming humpback whales to quantify maternal energy stores and offspring growth. By determining relative width measurements (width : length ratio) at multiple locations along the body, at two different stages of the migration, I illustrated that the location mid-way along the body (at 50% of the body length from tip of rostrum to tail notch) is a dominant energy storage site that can be used as an index for estimating body condition. By comparing this metric within and between seasons I determined that the body condition of lactating cows declined at different rates each year, decreasing at a mean rate of 0.36 cm/day in 2013 and 0.65 cm/day in 2015. Calf growth rate also differed each year, with calf body length increasing at a rate of 3.1 and 2.4 cm/day during early development in 2013 and 2015, respectively. These findings illustrate annual variations in maternal energy reserves and calf growth and highlight the influence of maternal investment on the growth and development of young baleen whale calves. Furthermore, this study provides a reliable technique of estimating the body condition of live whales that can be used to build a time series

of humpback whale health and its variability between years. Such fluctuations can provide valuable information about prey availability in the feeding grounds that can be used to indicate ecosystem health. This information can be compared with historical values to investigate biological responses to a changing climate.

During the photogrammetric study above, I made opportunistic observations of small calves at an area considered to be outside the recognised calving grounds of the BSD population. From these observations I classified the developmental stage of the calves according to their colour and size. Combined with behavioural data and survey details, I estimated that a minimum of ~20% of the expected number of calves in the population were born near, or south of, North West Cape on the Western Australian coast. As this location is situated 1000 km southwest of the recognised calving grounds (on the Kimberley coast of Western Australia), these findings illustrate geographical expansions that can take place as populations increase. For the BSD humpback whale population, the expansion of calving areas represents the re-colonisation of areas that were documented as being used previously, i.e. during the commercial whaling era. These expansions may begin to overlap with areas of high anthropogenic activity, particularly in areas of high human use such as coastlines or coral reefs. This highlights the need for monitoring the location and extent of calving and breeding areas as baleen whales recover from near extinction during the commercial whaling era last century.

By using two different methods of quantifying energy stores, I have created a unique time series of cetacean body condition that spans multiple eras. Historical whaling records have provided a measure to quantify cetacean energy stores and their variation within and between species, demonstrating the substantial energy stores required by capital breeders to complete their annual migration. Photogrammetric techniques have provided a method to quantify energy stores of free-swimming whales during the annual migration, demonstrating that maternal energy stores vary between years and influence offspring growth and

development. Information on energy stores can be used to assess individual or population health in a recovering population or expanded over time to monitor biological response to environmental change. Identifying the expanded extent of the BSD humpback whale population has highlighted the need for monitoring the location and extent of calving areas to allow appropriate management of important habitat, particularly where high levels of anthropogenic activity may occur.

Statement of Publication and Co-authorship

Chapters 2 & 4 are produced from manuscripts published in peer reviewed journals.
Chapter 3 is in preparation for submission to a peer reviewed journal.

The following people and institutions contributed to the publication of the work undertaken as part of this thesis:

Lynette Irvine, University of Tasmania = **Candidate**

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The candidate was responsible for the study design, data analysis, fieldwork, interpretation of the results and manuscript preparation in all of the following manuscripts. In addition, the candidate located the historical whaling data set used in manuscript 1.

Manuscript 1 Lyn G. Irvine, Michele Thums, Christine E. Hanson, Clive R. McMahon, Mark A. Hindell (2017). Quantifying the energy stores of capital breeding humpback whales and income breeding sperm whales using historical whaling records. *Royal Society Open Science*, 4,160290

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We the undersigned agree with the above stated “proportion of work undertaken” for each of the above published (or in preparation for publication) peer-reviewed manuscripts contributing to this thesis.

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Chapter 1

General Introduction

1.1 Animal migration

Migration is a common phenomenon in the animal kingdom that has evolved repeatedly and independently amongst a broad range of taxa including insects (Southwood, 1962), crustaceans (Bauer, 2013), amphibians (Sinsch, 1990), fish (Harden Jones, 1968), reptiles (Southwood and Avens, 2010), birds (Lack, 1968) and mammals (Lockyer and Brown, 1981). It has evolved as an adaptation to spatiotemporal variation in resources or risks (Southwood, 1962, Dingle and Drake, 2007), and the need for different habitats and resources at different life stages (Alerstam et al., 2003, Dingle and Drake, 2007).

The huge diversity in migratory organisms has resulted in migration being defined by multiple authors in many different ways. Definitions range from the simple to the more complex depending on whether individuals or populations are being referred to and whether the function or form of migration is being described. For example, based on observations of terrestrial insect populations, Southwood (1962) defined migration as "movement between different habitats". In contrast, Kennedy (1985) observed the flight behaviour of individual aphids (*Aphis fabae*) and defined migration as "persistent and straightened-out movement affected by the animals own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station keeping responses, but promotes their eventual disinhibition and recurrence" (Kennedy, 1985).

In this thesis, I study migration at the population level and consider it to be the movement of organisms between different habitats in a manner synchronised with the seasonal cycle. Migration occurs because this movement offers higher

fitness benefits to organisms compared to remaining in one place (residency). Successful migration requires attaining resources essential for survival and reproduction, such as food, mates or suitable breeding areas, avoiding threats, such as predators (Fryxell et al., 1988, Bollens and Frost, 1989, Corkeron and Connor, 1999, Hebblewhite and Merrill, 2007, McKinnon et al., 2010), parasites (Folstad et al., 1991) and competition (Kelly et al., 2002).

1.1.1 Types of migration

Migration can take many forms and occur across different types of environments, including air, water and land. For example, daily vertical migrations within the water column are undertaken by aquatic organisms such as zooplankton (Bollens and Frost, 1989); altitudinal migrations between different elevations are carried out by terrestrial organisms such as deer (Mysterud, 1999); diadromic migrations between fresh and salt water are undertaken by fish species such as salmon (Hodgson et al., 2006) and crustaceans such as shrimp (Bauer, 2013); and annual migrations between different geographical locations are undertaken by a myriad of organisms including birds (Lack, 1968), butterflies (Gibo and Pallett, 1979) and baleen whales (Dawbin, 1956, Chittleborough, 1965).

Migration varies both between species and within species. For example, some species undergo partial migrations where some individuals in the population remain in the same area all year round (i.e. resident) while others move away (Mysterud et al., 2011). Other species undergo differential migration where some components of the population (e.g. different age groups, reproductive classes, or sexes) migrate to different areas than others (Lack, 1968).

1.1.2 Scales of migration

Migrations are undertaken on a variety of different scales, depending largely on the mode of locomotion, but also on body size, energy stores, and travel speed (Alexander, 1998). Vertebrate locomotion occurs in three different modes, namely swimming, running, and flying. Each of these modes involves different mechanical movements and each has its own particular energetic costs (Schmidt-Nielsen, 1972). Accounting for body size, swimming migrants have the lowest cost of travel, while flying and running migrants use approximately three and ten times more energy respectively (Schmidt-Nielsen, 1972, Alexander, 2003, Åkesson and Hedenström, 2007).

Flying and swimming migrants have the advantage of travelling in a moving medium, which can be used to reduce the cost of travel. For example, flyers can use winds (Liechti, 2006, Chapman et al., 2008) and thermal updrafts (Pennycuick, 1969, Gibo and Pallett, 1979) to reduce their energetic costs, while swimmers can use currents (Luschi et al., 2003b), tidal movements (Hunter et al., 2004) and stream flows (Standen et al., 2004). As a result, flyers and swimmers are capable of carrying out global migrations of tens of thousands of kilometres, while terrestrial migrants are generally limited to migrations in the order of hundreds of kilometres. For example, the longest known migration is that of the Arctic tern (*Sterna paradisaea*) which migrates up to ~80,000 km between the Arctic and the Antarctic, traversing the Atlantic Ocean (Egevang et al., 2010). Other long-distance migratory seabirds include sooty shearwaters (*Puffinus griseus*) and short-tailed shearwaters (*Ardenna tenuirostris*), which travel ~64,000 km and ~60,000 km, respectively, on trans-equatorial migrations that traverse the Pacific Ocean (Shaffer et al., 2006, Carey et al., 2014). Swimmers such as white sharks (*Carcharodon carcharias*) and Atlantic bluefin tuna (*Thunnus thynnus*) undertake transoceanic migrations of up to 11,000 km across the Indian (Bonfil et al., 2005) and Atlantic oceans (Block et al., 2005). In comparison, the longest known

migration of a terrestrial migrant is that of the caribou (*Rangifer tarandus*), which travels a one-way distance of 1200 km (Alerstam et al., 2003), while the famous migrations of the large wildebeest (*Connochaetes taurinus*) herds are about 200 km (Dingle, 1996).

1.1.3 Annual migration

Probably the most well-known migrations in the animal kingdom are annual migrations that involve movement between different geographical areas. These migrations are typically carried out between breeding and non-breeding locations and are synchronised to the seasonal cycle. These migrations include the extensive journeys of the great whales that traverse ocean basins between polar feeding grounds and tropical breeding grounds (Dawbin, 1956, Chittleborough, 1965), and the huge herds of wildebeest that move hundreds of kilometres across the African savannah following rainfall events (Holdo et al., 2009). Lesser known, but no less important, are the annual migrations of animals such as birds (Lack, 1968), turtles (Luschi et al., 2003a) and insects (Southwood, 1962), including monarch butterflies and desert locusts.

Synchronising movements with the seasonal cycle enables access to resources that are temporarily available and use of areas where physical conditions may be appropriate only at certain times of the year, or for certain periods of the lifecycle. For example, some migrants follow food resources across different geographical regions, timing their arrival to coincide with beneficial seasonal events, such as the ripening of energy rich fruits or the emergence of protein rich insects (Izhaki and Safriel, 1985). Numerous 'staging migrant' bird species follow this strategy, feeding at multiple stopover sites along their migration route, and topping up their energy stores on energy rich foods (Beekman et al., 1991). Similarly, ungulates follow high quality feeding patches after rainfall events (Holdo et al., 2009). Other migrants de-couple feeding and breeding activities completely, enabling life

histories that consist of either i) marine feeding periods and terrestrial breeding periods, such as the pinnipeds (Costa, 1991); or ii) utilising different geographical areas for feeding and breeding, such as the baleen whales (Lockyer and Brown, 1981).

1.1.4 Migration Cues

The timing of migration onset is crucial for successful migration as it initiates the annual cycle that requires precise temporal synchrony between migrant and resources. Circannual rhythms regulated by photoperiod are generally accepted as a large driver for migration onset among all vertebrates (Gwinner, 1996, Gwinner, 2003, Dardente et al., 2010). However, migration onset does not occur on exactly the same day each year signifying that exogenous environmental factors are also involved. Environmental conditions at the departure location have been shown to influence the departure date of migratory birds (Marra et al., 1998, Shamoun-Baranes et al., 2006, Studds and Marra, 2007), leading to the suggestion that the final decision for departure date is fine-tuned by environmental conditions at the departure site (Gordo, 2007).

Environmental conditions can affect migration onset directly or indirectly through processes that affect migrant physiological condition. For example adverse weather conditions such as strong head winds have been shown to delay departure in migratory birds (Battley, 1997), while favourable winds have triggered early departure (Conklin and Battley, 2011). High rainfall has been shown to advance departure through improved migrant body condition resulting from increased food supply (Studds and Marra, 2007). In fact, it has been shown that physiological condition is a major determinant of departure time, with migrants in better physical condition leaving the feeding grounds sooner than those in poorer condition (Marra et al., 1998, Bridge et al., 2010, Goymann et al., 2010). Studds and Marra (2007) hypothesised that endogenous cues would trigger

migratory restlessness, but migratory onset would not take place until migrant body condition was sufficient to survive the migration. Craig et al. (2003) suggested that in humpback whales (*Megaptera novaeangliae*), a complex interaction between photoperiod, hormonal state, body condition and food availability may underpin the timing of the migration, and in fact whether an individual actually migrates from the feeding grounds at all (Craig et al., 2003). As humpback whales accumulate all of the energy for their migration prior to leaving the feeding grounds, it is likely that body condition plays a major role in their departure decision.

1.1.5 Long-distance migration

Breeding and non-breeding or feeding areas may be separated by large distances (100s to 1000s of km). Long-distance migrations are energetically expensive, regardless of whether they occur in air, water or on land, and often require substantial preparation. Preparation differs according to the mode of travel being used, the distance being travelled and the feeding opportunities *en route*. Airborne migrants, for example, need to prepare their bodies for flight, which can involve growing larger wings, strengthening flight muscles and supressing non-essential organs to minimise body weight (Dingle, 2006). Migrants that have limited or no feeding opportunities along their migratory route need to prepare their bodies for long periods of fasting by accumulating large energy stores (Lockyer and Brown, 1981, Kwan, 1994, Brower et al., 2006). For these migrants, energy storage prior to departure can be substantial in terms of both quantity and effort. For example, on departure for their 11,000 km annual migration, 55% of the body mass of bar-tailed godwits (*Limosa lapponica*) is made up of fat stores (Piersma and Gill, 1998, Gill et al., 2005). Similarly, humpback whales can double their weight over the feeding season (Lockyer, 1981b) by spending 4.5 - 6.5 months in the feeding grounds (Dawbin, 1966) and depositing up to 900 kg of fat per week (Ash, 1953).

1.1.6 Energy demands and energy stores

Large animals have lower mass specific energy requirements and higher energy storage potential than smaller animals, as maintenance metabolism is proportional to surface area (~mass$^{0.75}$) while energy stores are proportional to body size or volume (mass$^{1.0}$) (Brodie, 1975, Calder, 1984, Millar and Hickling, 1990). Thus, smaller animals have higher mass-specific metabolic costs than larger animals (Brodie, 1975, Millar and Hickling, 1990) and therefore require a higher relative energy intake. For example, the smallest marine mammal, the sea otter (*Enhydra lutis*) requires a daily food intake of 20-25% of body mass each day (Morrison et al., 1974), compared to the southern elephant seal (*Mirounga leonina*) that requires just 7%. Large body size is thus advantageous for long-distance migration as large energy storage potential alleviates the need for regular food intake along the migratory route.

Energy stores are critical for long distant migrants as they must often satisfy the costs incurred during migration whilst enduring long periods of fasting. Energy stores influence fasting capabilities (Lindstedt and Boyce, 1985, Millar and Hickling, 1990) and thus the duration and distance of migration (Bridge et al., 2010). They also influence individual survival and population sustainability (Hindell and Slip, 1997, Clausius et al., 2017b, McMahon et al., 2017) through their effects on individual fitness, breeding success (Guinet et al., 1998, Norris et al., 2004), fecundity (Lockyer, 1986, Leaper et al., 2006), and foetal growth (Lockyer, 2007, Christiansen et al., 2014b). Where no feeding opportunities are available *en-route*, sufficient energy reserves must be accumulated in the foraging grounds, prior to departure, to fuel the entire annual migration including all en-route activities essential for survival and reproduction. The energy stores required for long-distance migrations varies between reproductive and age groups, depending on the different activities undertaken on the journey, such as metabolism, growth, mating, gestation, and lactation (Fortune et al., 2013).

1.1.7 Life history

Energy not used in essential maintenance functions such as metabolism can be allocated to other activities such as growth, travel or reproduction. Species that fuel reproduction with stored energy are termed 'capital breeders', while those that reproduce using energy accrued on a continual basis are termed 'income breeders' (Jönsson, 1997, Stearns, 1989). The capital breeding strategy facilitates long-distance migrations as energy can be accumulated in areas where food resources are abundant and transported to other areas where food resources are limited or non-existent. However, this strategy requires the transportation of large energy stores and relies on abundant food reserves in the feeding grounds (Stephens et al., 2014). Income breeding on the other hand does not require transportation of large fuel loads, but instead requires stable or predictable environments (Costa, 1993, Oftedal, 1997) that provide regular and frequent feeding opportunities.

Many organisms use a mixture of the two strategies by accumulating large energy stores prior to departure from the feeding grounds, and topping up on supplementary food resources available along the migratory path and/or at the arrival destination (Drent et al., 2006, Wheatley et al., 2008). Many bird species use this strategy, using multiple 'staging' points along their migratory path to top up their energy stores during migration rather than overloading their bodies with weight at departure. Some birds, such as the bar-tailed godwit that travels 11,000 km with no stopover (Gill et al., 2005) use the capital breeding strategy, but this is quite rare. The capital breeding strategy is more common amongst aquatic organisms, such as European eels (van Ginneken and van den Thillart, 2000, van Ginneken et al., 2005), phocid seals (Costa, 1991) and baleen whales (Lockyer and Brown, 1981), due to their low cost of transport (Houston et al., 2007).

1.1.8 Baleen whale migration

Baleen whales, with their large body size and relatively low cost of transport, are perfectly adapted for capital breeding. Many baleen whales migrate thousands of kilometres each year between high latitude feeding grounds and low latitude breeding grounds, on round-trip journeys that can take up to 6-8 months (Dawbin, 1956, Chittleborough, 1965). The reasons for their long-distance migrations however, are poorly understood and have been the topic of much debate (e.g. Corkeron and Connor, 1999, Clapham, 2001). Numerous hypotheses have been suggested to explain these migrations, including resource tracking (Payne, 1995), remnant evolutionary behaviour (Evans, 1987), predator avoidance (Corkeron and Connor, 1999), energetic benefits of warm water for adults (Brodie, 1975) and calves (Costa and Williams, 1999, Clapham, 2001), and calm water for calves (Norris, 1967). However, the evidence for each of the arguments remains equivocal and no single explanation has emerged to dominate the debate. Although inconclusive, the most common hypotheses are those based on survival benefits for the calves, namely i) travelling to the warm waters of the tropical breeding grounds for a thermoregulatory benefit, particularly for the young calves (Clapham, 2001); and ii) travelling away from areas of high killer whale (*Orcinus orca*) abundance in the higher latitudes to minimise predation pressure (Corkeron and Connor, 1999), particularly on the newborn calves.

1.1.8.1 Calving Grounds

Calving grounds are critical components in the lifecycle of baleen whales as they have the dual role of providing protection for young, weak calves when they are at the most vulnerable stage in their life history (Gabriele et al., 2001), and providing a calm environment for the mothers who must conserve energy during extended periods of simultaneous fasting and lactation (Gittleman and Thompson, 1988). These areas must provide habitat that is suitable for efficient thermoregulation

and efficient transfer of energy from mother to offspring in order to maximise calf growth. Globally, humpback whale breeding grounds are distributed within 30° of the equator in waters between 21.2°C and 28.3°C (Rasmussen et al., 2007). While there is emerging evidence that sea mounts may be important breeding areas (Carrigue et al., 2015), females typically prefer the shallow, protected waters of coastal areas, islands and offshore shoals for mating and calving (Mattila and Clapham, 1989, Alison and Louis, 2000, Ersts and Rosenbaum, 2003, Félix and Botero-Acosta, 2011). However, as for many marine mammals, their cryptic and highly mobile marine existence means that the location of the calving areas are not well known for any population (Harwood, 2001).

1.1.9 Humpback whale migration

Humpback whales travel up to 19,000 km annually on the longest migration of all mammals (Robbins et al., 2011). This vast migration is preceded by months of intensive feeding in productive, polar waters, in preparation for movement into the distant, oligotrophic breeding grounds. During the journey, and on the breeding grounds, fasting can last for up to 8 months (Dawbin, 1966, Lockyer and Brown, 1981). During this time all survival and reproductive activities are fuelled by energy reserves accumulated previously in the feeding grounds. As with all baleen whales, the time spent in the feeding and breeding grounds varies with reproductive class, according to the energetic demands of the different activities undertaken during the journey (Lockyer, 1981b, Fortune et al., 2013). The average stay in the Antarctic foraging grounds for non-breeding females, mature males and immature animals is 5.5 months; for lactating females accompanied by calves it is 4.5 months; while that for pregnant females is 6.5 months (Dawbin, 1966).

As a result of these varying time periods spent in the foraging grounds, the humpback whale migration is segregated temporally by age class, sex and reproductive status (Chittleborough, 1965, Dawbin, 1966, 1997). Lactating females

with their yearling calves are the first cohort to leave the Antarctic foraging grounds, followed by immature whales of both sexes, mature males and non-pregnant mature females, with pregnant females the last to depart. Departure from the tropical breeding grounds is much the same order, except for the newly-pregnant females who leave first with the non-pregnant females and juveniles, followed by mature males and, then finally, females with newborn calves (Dawbin, 1997). As pregnant females arrive in the Antarctic first and leave last (Dawbin, 1956, Chittleborough, 1965, Dawbin, 1997), they get additional time in the foraging grounds to accumulate the large energy reserves required for gestation and lactation the following breeding season (Lockyer, 1981b, Irvine et al., 2017b).

1.1.9.1 Breeding Stock D population

Humpback whales are a cosmopolitan species inhabiting all of the world's oceans. Populations are geographically separated into those from the North Atlantic, North Pacific and Southern Hemisphere, with seven distinct populations being recognised in the Southern Hemisphere (IWC, 2011). The Breeding Stock D (BSD) population undertakes annual migrations of 14,000 km (Double et al., 2010) between its feeding grounds in Antarctic waters and breeding grounds in tropical waters along the Western Australian coast (Chittleborough, 1965).

There have been numerous abundance estimates of this population over the years, in both the breeding grounds and feeding grounds (Table 1.1). The estimates from the Antarctic feeding grounds have generally been higher than those from the breeding grounds, leading to the suggestion that a portion of the population does not migrate to the breeding grounds every year (Branch, 2011). Although the abundance estimates are varied, they illustrate that the population has increased from an estimated 568 individuals at the end of 1963 (Bannister, 1964) to approximately 18,000 - 26,000 individuals in 2008 (Hedley et al., 2011, Salgado Kent et al., 2012). This represents a population increase of about 10-13%

per year, a rate which is at, or just above, the maximum plausible level (Zerbini et al., 2010).

Table 1.1 Abundance estimates of the Breeding Stock D population in breeding grounds (along the western Australian coast) and feeding grounds (Antarctica, area IV: 70°E-130°E).

Year	Abundance estimate	Survey area	Location	Reference
1963	568	Breeding grounds	Carnarvon	(Bannister, 1964)
1994	4,000 - 5,000	Breeding grounds	Shark Bay	(Bannister, 1995)
1999	8,207 - 13,640	Breeding grounds	Shark Bay	(Bannister and Hedley, 2001)
2005	6,700 - 24,500	Breeding grounds	Shark Bay	(Paxton et al., 2011)
2008	14,210 - 27,720	Breeding grounds	Shark Bay	(Hedley et al., 2011)
2008	20,152 - 33,272	Breeding grounds	North West Cape	(Salgado Kent et al., 2012)
1978/79	968 (CV=0.45)	Feeding grounds	Antarctica, Area IV	(Branch, 2011)
1988/89	3,809 (CV=0.52)	Feeding grounds	Antarctica, Area IV	(Branch, 2011)
1997/98	17,938 (CV=0.18)	Feeding grounds	Antarctica, Area IV	(Branch, 2011)

The BSD population was subject to extensive exploitation in the 20th century with commercial whaling operations (legal and illegal) occurring in both the breeding and feeding areas during a number of different eras. Coastal whaling occurred in the breeding grounds along the Western Australian coast from 1912 - 1916, from 1925 - 1928 and from 1936 - 1938 (Ruud, 1952), while whaling in the Antarctic feeding grounds occurred between 1934 and 1939 (Jonsgard et al., 1957). The last phase of legal commercial whaling on this population occurred between 1949 and 1963, when a total of 18,180 humpback whales were killed in the Antarctic feeding grounds (5,868) and at three whaling stations along the Western Australian coast (12,312) (Chittleborough, 1965, Allison, 2013). In addition to this, Soviet vessels carried out illegal whaling operations that killed a further 9,021 BSD humpback whales between 1957 and 1968 (Clapham et al., 2009). By the time a moratorium was introduced in 1963 to protect them from hunting, the population had been reduced to an estimated 568 individuals, of which only 261 were considered to be adults (Bannister, 1964). Although commercial hunting drove the species to near extinction, it has left behind an extensive trail of biological information that can be

used for conservation purposes in modern day science. The recovering BSD population now travels freely along the Western Australian coast in nearshore waters, resulting in large numbers of free-swimming humpback whales being easily accessible for non-lethal sampling during their annual migration.

1.2 Body Condition

Body condition is a measure of the energetic status of an animal, indicated by the size of energy reserves accumulated through feeding (Schulte-Hostedde et al., 2001, Peig and Green, 2009). These energy reserves, stored mainly as fat, can have important fitness consequences for an individual. For example, in marine mammals, body condition has been shown to affect foraging ability (Irvine et al., 2000), reproductive success (Guinet et al., 1998) and competition for mates (Anderson and Fedak, 1985), and thus potentially plays an important role in the regulation of population size (Hindell and Slip, 1997). Body condition has traditionally been described by body composition, i.e. quantifying relative amounts of the five main components of body composition: water, fat, protein, carbohydrates and inorganic constituents (Reynolds and Kunz, 2001). The values of these five components are often combined into broader categories such as fat and lean mass (water, protein, carbohydrates and inorganic constituents) or fat, water and lean dry mass (protein, carbohydrates and inorganic constituents) according to researcher needs (Reynolds and Kunz, 2001). Although this method is very informative, it involves measuring the mass of each body component, and thus requires lethal sampling.

A range of 'condition indexes' have been devised as an alternative to traditional body composition analyses, enabling body condition assessments of live animals and also repeat measurements of the same individual. Such condition indexes include body composition analyses that use non-destructive methods, such as ultrasonography (e.g. Gales and Burton, 1987), isotope dilution (e.g. Slip et al.,

1992) and bioelectrical impedance (BIA) (e.g. Tierney et al., 2001). Other condition indexes include biochemical indexes such as hormonal status (e.g. Wingfield et al., 1992) and DNA investigation (e.g. Clemmesen et al., 2003) and morphological indexes that describe body size, shape and mass (e.g. Cattet and Obbard, 2005).

Morphometric condition indexes are commonly used in ecological studies as they are non-lethal and often quick and practical to conduct in the field (Stevenson and Woods, 2006). They are generally based on a measure of mass and skeletal size, and rely on the assumption that individuals of similar body condition will share the same relationship between body mass and body size. Any variation from this relationship is interpreted as a variation in body condition. Many morphometric condition indexes have been devised, on a range of species, with the relative merits of each index being the subject of considerable discussion (e.g. Jakob et al., 1996, Schulte-Hostedde et al., 2005, Peig and Green, 2010).

1.2.1 Methods for determining cetacean body condition

Quantifying the body condition of cetaceans can be a difficult task as their large body size and marine lifestyle typically prevents capture for measurement. Various methods, including biochemical tissue analysis and quantification of anatomical measurements such as body lipid, blubber thickness, blubber volume, and body girth (Lockyer et al., 1985, Lockyer, 1986, Lockyer, 1991, Víkingsson, 1995, Ichii et al., 1998, Næss et al., 1998, Haug et al., 2002, Evans et al., 2003, Irvine et al., 2017b, Lockyer, 1981b), have been used to assess cetacean body condition. However, these methods typically require the animal to be deceased before sampling, and are thus limited to samples from commercial whaling (Chittleborough, 1965, Lockyer, 1981b, Irvine et al., 2017b), animal strandings (Evans et al., 2003), or programs involving lethal sampling (e.g. Konishi et al., 2008, Konishi et al., 2014). A ban on commercial whaling and ethical concerns around

lethal sampling (Gales et al., 2007, Gales et al., 2008) necessitate the use of alternative non-lethal methods.

An alternative method, that of measuring blubber thickness by ultrasound, has been used on large marine mammals, including Elephant seals (*Mirounga leonina*) (Gales and Burton, 1987) and whales (Miller et al., 2011), but the method requires close access to animals and at times risky procedures such as anaesthesia (Gales and Burton, 1987). A method that has much potential, but has been under-utilised to date, is photogrammetry - the science of measuring photographs. Photogrammetry is a sampling method that can be applied remotely, is non-lethal, non-invasive and is capable of capturing detailed information on large numbers of individuals (Bell et al., 1997). It has been used successfully to determine the relative body condition of a range of baleen whales, including grey (*Eschrichtius robustus*), right (*Eubalaena glacialis, E. australis*), humpback and blue whales (*Balaenoptera musculus*) (Perryman and Lynn, 2002, Miller et al., 2012, Christiansen et al., 2016, Durban et al., 2016). It is ideal for cetacean research as it uses morphometric measurements such as width (a proxy for girth), which is considered to be one of the best methods of estimating cetacean body condition (Rice and Wolman, 1971, Lockyer, 1986, Lockyer, 1987) as it accounts for fat stored in multiple body tissues including the blubber, muscle and viscera (Slijper, 1962, Lockyer, 1981b, Lockyer, 1991). The method has been validated by Miller et al., (2012), who found that girth (diameter) measurements of right whale carcasses were comparable with diameter from photogrammetric width measurements.

A range of different approaches have been used to describe the relative body condition of cetaceans by photogrammetric methods. Some researchers have measured width at the widest point of the body (e.g. Perryman and Lynn, 2002), or at a defined location along the body (e.g. Durban et al., 2016) based on the assumption that these locations are areas of energy storage. Other researchers

have measured width at multiple locations along the body to get a more complete picture of body shape and areas of energy storage (e.g. Miller et al., 2012). Further variations include estimates of body surface area (Christiansen et al., 2016) and body volume (Christiansen et al., 2018). The best measure of body condition is difficult to identify, as it is rarely possible to validate these photogrammetric body condition indexes with data on body composition.

1.3 Research Objectives

Information on the energetics of capital breeders is fundamental to the understanding of long-distance migration and the strategies required for survival and reproduction during extensive journeys away from foraging areas. Examining energy stores between and among species, particularly those with different life histories (e.g. income and capital breeders), can reveal varying patterns of energy accrual and allocation that can contribute to a broader understanding of the energetic tactics of successful migration. Cetaceans are ideal candidates for such investigations as they exhibit a range of life history strategies and some have a huge body size that allows for large energy stores relative to metabolic demands. In particular the baleen whales undertake an extreme form of migration that is unprecedented amongst all mammals.

The primary aim of this thesis was to improve our understanding of the energetic strategies of the capital breeding humpback whale during the annual long-distance migration between the feeding and breeding grounds. This aim is addressed in three research chapters, each of which addresses a key objective, followed by a final chapter which draws them together in a general discussion. A brief overview of each chapter is presented below:

Chapter 2: Cetacean energy stores

Key objective: Quantify the energy stores of cetaceans with different life history strategies

Synopsis: I located a hitherto forgotten and unique handwritten historical whaling dataset from the company records of the Cheynes Beach Whaling Company in Western Australia. These records included individual oil yield measurements of sperm and humpback whales processed at the Cheynes Beach whaling station between 1952 and 1963. Unlike most whaling stations, oil at this station was extracted from the entire carcass, thus providing a measure of total body lipid and a rare opportunity to quantify cetacean energy stores of two large cetaceans with different life history strategies. I developed relationships between length and oil yield that illustrated the large energy storage potential of large body size, the considerable energy demands of long-distance migration and the high energy demands of reproduction in capital breeders. These relationships highlighted specific cohorts, such as small juveniles and small breeding females that are vulnerable to energetic stress during long-distance migration. Importantly, these relationships provide highly valuable contributions to ecosystem and bioenergetics models. This is particularly important, given that data of this detail and extent is unlikely to ever be collected again.

Chapter 3: The cost of lactation

Key objective: Quantify the costs of lactation in the breeding grounds

Synopsis: I took vertical aerial photographs of free-swimming humpback whales, during their northern and southern migration along the Western Australian coast, to quantify the use of maternal energy stores and calf growth during lactation.

Using photogrammetric methods, I introduced a reliable method of quantifying the body condition of large cetaceans, and their accompanying calves, without the need to handle, or gain close access to, the animals. By quantifying the rate of cow body condition decline and calf growth in the breeding grounds in two separate years, I identified previously undocumented annual differences in maternal investment and growth rates of dependent calves. The identified implications of this variability include impacts on offspring survival, future reproductive success and population dynamics. Importantly, this study illustrated that cetacean energy stores can be accurately quantified by photogrammetric methods and thus that invasive or lethal methods are not necessary in modern day science.

Chapter 4: Humpback whale calving areas

Key objective: Determine the calving range of the BSD humpback whale population

Synopsis: I used photogrammetric methods to classify the developmental stage of small calves observed at North West Cape, along the Western Australian coast. As these calves were observed a substantial distance south of the recognised calving areas of the BSD population, age estimation was essential for investigating their occurrence in the region (i.e. establishing whether the calves were born in the region or were older calves travelling southwards after being born earlier in calving grounds to the north). The classification of the calves as neonates, coupled with their persistent northward movement demonstrated that they were in fact born in the region of North West Cape, at least 1000 km south of the recognised calving areas along the Kimberley coast. When combined with population estimates, my results illustrated that approximately 20% of the expected calving population was born south of the currently recognised calving areas, thus

providing strong evidence for the expansion of the recognised calving grounds of the BSD population. The identified implications of such range expansions for recovering populations include differing travel costs and metabolic costs from residing in waters of different temperatures. They also include potential costs from overlap with areas of high anthropogenic activity. This is particularly important for mothers and calves who prefer shallow, protected locations along coastlines or around islands.

1.4 Thesis Structure

This thesis has been written as a series of separate manuscripts with a number of co-authors from the Institute for Marine and Antarctic Studies, Australian Institute of Marine Science, Sydney Institute of Marine Science, BMT Oceanica and Curtin University. Other than this introductory chapter and the final discussion, each chapter has been written as a scientific manuscript that has been published or is in preparation for submission. Consequently, there may be some overlap of text and ideas between chapters. I was the senior author, responsible for experimental design, data collection, analysis and the writing of each manuscript. My co-authors contributed to experimental design, data analysis and critical review of the manuscripts for publication. The co-authors are listed with the title and journal reference at the start of each chapter and their contribution is detailed in the statement of publication and co-authorship. A single bibliography is presented at the end of the thesis using the Harvard referencing style.

Chapter 2

Quantifying the energy stores of capital breeding humpback whales and income breeding sperm whales using historical whaling records

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2.1 Abstract

Cetacean energy stores are known to vary according to life history, reproductive status and time of year; however, the opportunity to quantify these relationships is rare. Using a unique set of historical whaling records from Western Australia (1952 - 1963), we investigated energy stores of large cetaceans with differing life histories, and quantified the relationship between total body lipid and length for humpback whales (*Megaptera novaeangliae*) (n = 905) and sperm whales (*Physeter macrocephalus*) (n = 1961). We found that total body lipid increased with body length in both humpback and sperm whales, consistent with size-related energy stores. Male humpback whales stored 2.49 kl (15.6 barrels) (31.9 - 74.9%) more lipid than male sperm whales of equivalent length, to fuel their annual migration. Relative lipid stores of sperm whales (males) were constant throughout the year, while those of humpback whales varied with reproductive class and sampling date. Pregnant female humpback whales had higher relative energy stores than non-pregnant females and males (26.2% and 37.4%, respectively), to fuel the energy demands of gestation and lactation. Those that reached the sampling site later (*en route* to their breeding grounds) carried higher lipid stores than those that arrived earlier, possibly reflecting individual variation in residency times in the Antarctic feeding grounds. Importantly, longer pregnant females had relatively larger energy stores than the shorter pregnant females, indicating that the smaller individuals may experience higher levels of energetic stress during the migration fast. The relationships we developed between body lipid and length can be used to inform bioenergetics and ecosystem models when such detailed information is not available.

2.2 Introduction

To optimise their fitness, organisms must acquire and allocate resources over their lifetime in a way that maximises individual survival and reproduction (Stearns, 1989). A range of life history strategies have evolved to achieve this, with 'capital breeding' and 'income breeding' representing the extremes of a continuum in how individuals store and allocate maternal resources (Stearns, 1989, Jönsson, 1997). Capital breeders use stored energy for reproduction and survival, while income breeders use energy that is acquired on a continual basis, including during the reproductive period (Stearns, 1992, Stephens et al., 2009). Energy storage enables the temporal and spatial separation of different activities such as feeding and breeding (Jönsson, 1997) and hence utilisation of environments where resources such as food may be temporarily abundant, but where physical conditions may be unsuitable for successful reproduction (Alerstam et al., 2003, Dingle and Drake, 2007). The capital breeding strategy generally involves a lifecycle that consists of periods of intensive feeding and fasting that are synchronised with the annual seasonal cycle (Bertram et al., 2001, Visser et al., 2004, Both et al., 2010, Visser et al., 2011). For reproductive females, this strategy requires short periods of maternal care with high rates of energy flow to the young (Costa, 1991, 1993, Oftedal, 1997). The income breeding strategy of continuous energy acquisition throughout the year enables longer periods of maternal care (Costa, 1993, Oftedal, 1997), but requires stable or predictable environments.

Amongst mammals, the capital breeding strategy is restricted to large animals such as bears, true seals and baleen whales, due to the extreme energy demands of lactation during fasting (Costa, 1993, Oftedal, 1993) and relatively low mass specific energy requirements of large body size (Brodie, 1975). Cetaceans are theoretically ideal candidates for investigating energy storage strategies for different life histories, as their considerable body size enables large energy stores relative to reproductive demands (Oftedal, 1993). However,

in practice, this large body size combined with their marine existence prevents capture for measurement, making quantification of cetacean energy stores extremely difficult.

Among the cetaceans, baleen whales are typically capital breeders while toothed whales are generally income breeders (Oftedal, 1997). Many baleen whales, including humpbacks, move between productive high latitude feeding grounds during summer and relatively unproductive low latitude breeding grounds in winter (Dawbin, 1956, Chittleborough, 1965). This strategy requires the accumulation and storage of sufficient energy reserves to meet the cost of growth, maintenance, locomotion and reproduction in the breeding grounds (Jönsson, 1997). As reproductive costs are highest for breeding females, due to energy-expensive gestation and lactation (Oftedal, 1993), they require larger energy stores than males and non-pregnant females (Lockyer, 1981b, Perryman and Lynn, 2002, Bradford et al., 2012). By contrast, toothed whales typically meet their energy demands throughout the year by continual foraging (Lockyer, 1981a, Oftedal, 1997) and thus have no need to store large energy reserves. Consequently, the energy stores of capital and income breeders should differ: capital breeders (particularly pregnant females) should have high energy stores on departure from feeding grounds, followed by a continual decline in energy stores throughout the migration and the reproductive cycle (e.g. Rice and Wolman, 1971), until return to their feeding grounds; income breeders should have relatively constant energy stores throughout the year, given adequate food resources.

In cetaceans, energy is stored as lipid in various depots throughout the body, initially in the blubber, and then in the bone, muscle, and viscera (Slijper, 1962, Lockyer, 1981b). Cetacean energetics studies have typically focused on the blubber layer as it is an important and easily measured lipid store (e.g. Mellish et al., 2004, Miller et al., 2011). However, lipid storage in body tissues other than the blubber can be substantial (Brodie, 1975, Tonnessen and Johnsen,

1982, Lockyer et al., 1985) and should therefore also be considered. For example, muscle is a major lipid depot in both blue (*Balaenoptera musculus*) and fin (*Balaenoptera physalus*) whales (Lockyer, 1981b), and bone in fin whales can store nearly as much lipid as the blubber (Tomilin, 1957). Furthermore, analyses of the blubber layer can also be complicated by differences in thickness and lipid content at different sites along the body (Slijper, 1948, Lockyer et al., 1985, Lockyer, 1991, Naess et al., 1998), with no apparent correlation between the two (Evans et al., 2003). To obtain a complete picture of energy storage, lipid stores in all body tissues must ideally be accounted for. This however, can be impractical in large animals.

We recently located a historical whaling dataset from the Cheynes Beach Whaling Station, on the south coast of Western Australia. This whaling station, located about halfway along the migratory corridor of the Breeding Stock D (BSD) humpback whales (Jenner et al., 2001), processed humpback whales that were hunted between 1952 and 1963 (during their northward migration), and sperm whales hunted throughout the year between 1955 and 1976. Oil was extracted from the entire carcass[1], and detailed records of oil yield, length and sex were recorded for the majority (94.7%) of individuals processed between 1952 and 1963. After this time, the station expanded and oil yields were reported as weekly tallies. The individual catch records from 1952 - 1963 provide a unique dataset of individual whale oil yield that can be used to quantify total body lipid stores of two large cetaceans. The records from 1953 and 1954 have been used previously to quantify the relationship between humpback whale oil yield and body length (Chittleborough, 1965).

In this study we extend these analyses (Chittleborough, 1965) by using the individual catch records from Cheynes Beach Whaling Station to investigate how energy stores vary among cetaceans with different life histories. We compare

[1] Personal communication from Bruce Teede, Engineer (retired) Carnarvon Whaling Station, Babbage Island, Carnarvon, Western Australia, August 2016.

and quantify total body lipid of humpback whales and sperm whales to test the hypothesis that energy stores of humpback whales are higher than those of sperm whales due to their different life-history strategies. We then investigate the variation in body lipid of each species separately, according to body length, reproductive class and time of year, and produce equations to quantify these relationships. We predict that the energy stores of the income breeding sperm whales will remain constant throughout the year, while that of the capital breeding humpback whales will vary with the energy demands of each reproductive class. Chittleborough (1965) illustrated that pregnant female humpbacks had the largest energy stores due to the energy demands of pregnancy and lactation (Lockyer, 1981b). In addition to this, we predict that: i) mature, non-pregnant females will have variable energy stores due to their varying reproductive states, i.e. some are recovering from lactation while others are preparing for pregnancy; ii) mature males will have higher energy stores than the non-pregnant females, due to their need to compete for, and access, breeding females (Tyack and Whitehead, 1982, Baker and Herman, 1984); and iii) immature whales will have higher energy stores than mature males and mature non-pregnant females due to the high energy demands of growth (Fortune et al., 2013). Furthermore, as humpback whales spend the summer accumulating and storing body lipid at a rate of 200 l / week (Ash, 1957) and all migrate at the same speed (Dawbin, 1966), we predict that individuals sampled at Cheynes Beach Whaling Station later in the season will have higher energy stores than those sampled earlier.

2.3 Materials and methods

2.3.1 Data

Data were sourced from catch records that detailed 3000 individual whales processed at Cheynes Beach Whaling Station (35°05' S, 117°56' E): 961 humpback whales caught between 1952 and 1963; 2039 sperm whales caught

between 1955 and 1963 (supplementary material, table S1 in Appendix S1). Humpback whales were captured over the continental shelf, in waters generally less than 50 m deep (median = 13 m), while sperm whales were captured over the continental slope in waters generally 200 - 3000 m deep (median = 1067 m) (figure 2.1).

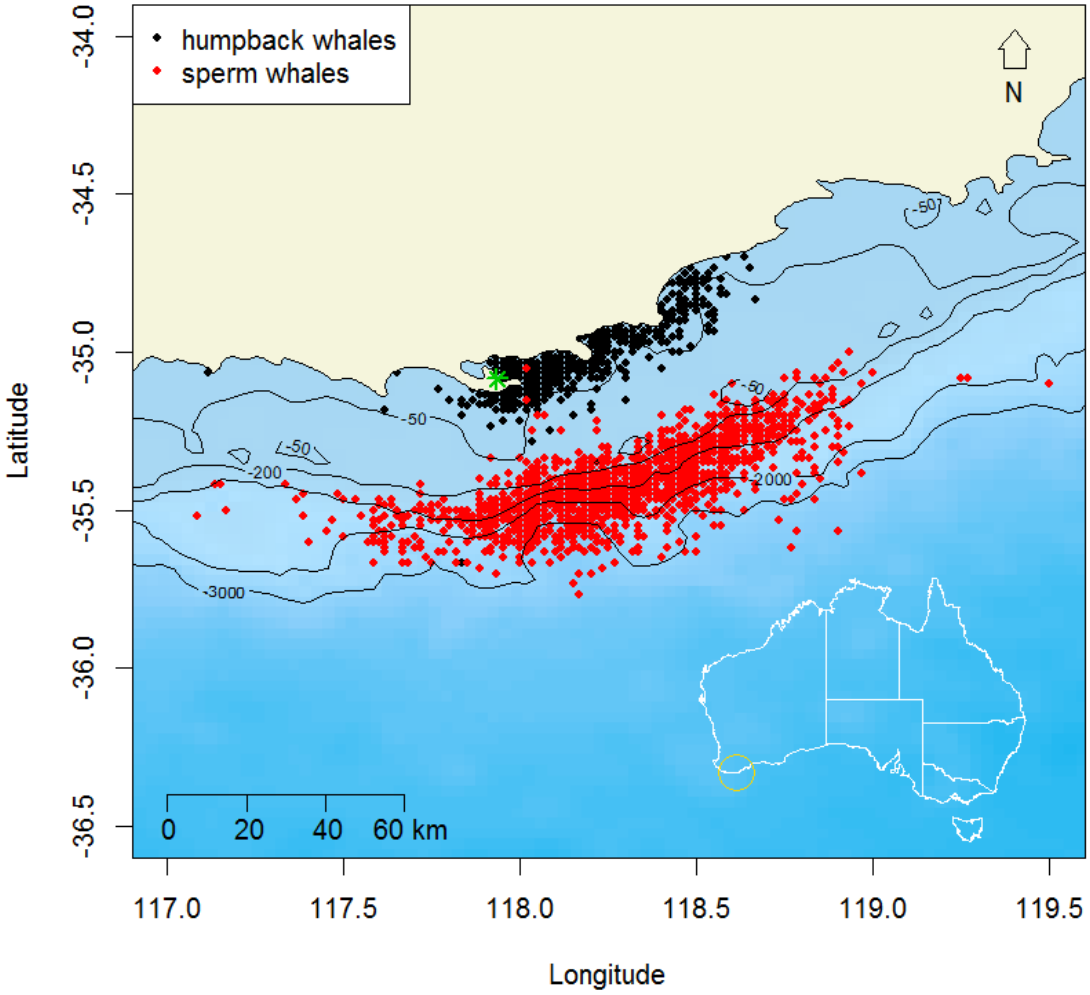

Figure 2.1. Location of Cheynes Beach Whaling Station (green asterisk), on the southwest coast of Western Australia, showing catch positions of humpback whales and sperm whales processed there between 1952 and 1963.

Humpback whales were caught between May and August, with highest catch numbers in July (figure 2.2). All humpbacks were caught on their northward migration between the Antarctic feeding grounds and lower latitude breeding grounds, as this population does not pass Cheynes Beach Whaling Station on

their return journey to Antarctic waters (Chittleborough, 1965). Sperm whales were caught in all months of the year, with a small peak occurring between April and May and a larger peak between September and November (figure 2.2). Sperm whale catches over summer (December - February) and winter (June - July) were low (figure 2.2) - the winter catch being influenced by the local availability of humpback whales at this time of the year (Bannister, 1964, 1968).

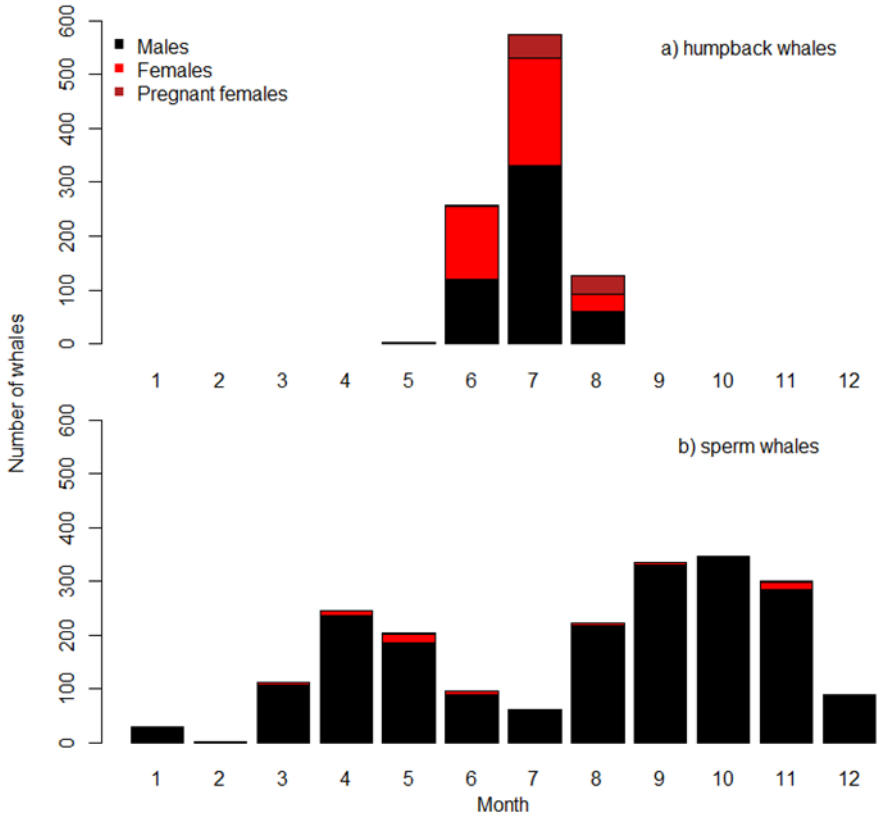

Figure 2.2. Number of (a) humpback whales and (b) sperm whales of each reproductive class (males, females and pregnant females) processed at Cheynes Beach Whaling Station each month during the years 1952 - 1963.

The catch records included individual details of catch date, location, whale length (recorded in feet), sex, oil yield (recorded in barrels) and length and sex of any foetus. We converted length into metres (1 ft = 0.3048 m) and oil yield into kilolitres (1 barrel = 0.16 kl (Tonnessen and Johnsen, 1982)). All data were checked for potential 'stretching', whereby whalers reported an undersized whale as longer than the actual size to avoid an infraction of the minimum size regulation (35 feet or 10.7 m) (Chittleborough, 1965, Clapham and Ivashchenko,

2016). We did this by constructing histograms of length and assessing the distribution to see if there was a notable peak around this minimum. Stretching was only identified for the female sperm whale data, and this was subsequently excluded from the analysis (accounting for 4% of total sperm whale data) (supplementary material, figure S1 in Appendix S1).

The measurement of total body lipid requires complete oil extraction from every part of the whale body. Oil extraction at Cheynes Beach Whaling Station was a two-step process carried out in large digesters. Initially the carcass was flensed for oil extraction from the blubber; then the remainder of the carcass was sawn into pieces and rendered for oil extraction from the muscle, bone and viscera.[2] Once the oil was recovered, meat meal and whale solubles were produced from the remaining residue (raw products such as whale meat were not produced at the Cheynes Beach Whaling Station (Frost, 1978)). Owing to this extraction process, the oil yield records for sperm whales included sperm oil from the body as well as spermaceti oil from the spermaceti organ. The implications of this are discussed in a later section.

2.4 Statistical analyses

To examine the relationship in total body lipid (kl) and body length (m) between and within the humpback and sperm whales, we constructed a suite of linear mixed-effects models, including all combinations of the individual predictor variables (described below) and their interactions. Year was included as a random effect to account for potential inter-annual variation in oil yield. All models were fitted in R (R v. 3.0.2) (R Development Core Team, 2013) using the packages *nlme* (Pinheiro et al., 2013) and *MuMIn* (Barton, 2014). We compared and ranked each model in the suite with Akaike's Information Criterion corrected for small samples (AIC*c*) and by their relative goodness-of-fit, the AIC*c*

[2] Personal communication from Bruce Teede, Engineer (retired) Carnarvon Whaling Station, Babbage Island, Carnarvon, Western Australia, August 2016.

weight (*w*AIC*c*) (Burnham et al., 2011, Burnham and Anderson, 2002) (Burnham and Anderson, 2002, Burnham et al., 2011). The AIC weight varies from 0 (no support) to 1 (complete support) relative to all models in the set (Burnham and Anderson, 2002). We also calculated the weights of the Bayesian Information Criterion (*w*BIC), and where the ranking did not agree with *w*AIC*c*, we used *w*BIC for model selection (as AIC frequently prefers a more complex model) (Link and Barker, 2006). Where models were within 2 AIC or BIC points of one another, they were considered equal and, under the principal of parsimony, the simplest model (one with the least terms) was selected. The proportion of variance in the response variable, explained for fixed factors ($R^2_{GLMM(m)}$) and fixed and random factors combined ($R^2_{GLMM(c)}$) (Nakagawa and Schielzeth, 2013), was used to quantify goodness-of-fit to the data (Burnham and Anderson, 2002).

2.4.1 Inter-species differences

We tested for differences in lipid stores between species by modelling total body lipid as a function of species and length. We had to restrict this analysis to males due to the unreliable length measurements of the female sperm whales. We also restricted the analysis to the length range common to both species (10.7 m (35 ft) - 14.2 m (46.5 ft)) and the years where both sperm and humpback whales were processed (1956 - 1962).

2.4.2 Intra-species differences

2.4.2.1 Humpback whales

To test for differences in lipid stores between reproductive classes, we modelled the relationship between total body lipid, length, and reproductive class (males, pregnant and non-pregnant females), using linear mixed-effects models. Male humpback whales < 11.2 m (36.75 ft) and females < 11.7 m (38.5 ft) were classified as immature whales (Chittleborough, 1965), and colour coded in the plots as a separate reproductive class. They could not be analysed separately as the range in their body length did not cover the range in body length for the

other classes. Given that the data were heterogeneous, with residuals increasing with body length, variance was weighted according to a power relationship of length (Zuur et al., 2009).

Humpback whale analyses were restricted to the months June - August and the years 1953 - 1962. Data from 1952 were excluded as factory efficiency in the first year of production was typically lower than in subsequent years (Chittleborough, 1965); data from years 1954, 1963 and May were excluded due to low sample size (supplementary material, table S1 in appendix S1). In 1955 body lengths were reported in feet only, rather than feet and inches as in all other years. To account for this, the dataset was analysed with and without the 1955 data. The results were the same with both analyses and thus the 1955 data were included in the final analysis.

To test our hypotheses regarding variation in energy stores through time, we modelled total body lipid as a function of length and month of catch. We analysed each reproductive class separately due to the temporally staggered migration of this population (Chittleborough, 1965). In addition, as the number of pregnant females and immature whales arriving in June and August respectively, were low, (supplementary material, table S1 in appendix S1), we restricted the analysis of the pregnant females to the months of July and August and that of immature whales to June and July. The lipid stores of the males and non-pregnant females were modelled over the full data range.

2.4.2.2 Sperm whales

We examined the relationship between total body lipid, length and season for male sperm whales only as female sperm whales had unreliable length measurements (as mentioned above). We used season (summer = Dec - Feb, autumn = Mar - May, winter = Jun - Aug, spring = Sep - Nov) as a fixed effect in the models, rather than month (as in the humpback whale analyses) because sample sizes were not sufficient in all months (supplementary material, table S1

in appendix S1). We restricted the analysis to 1956 - 1963 as the sample size in 1955 was too low (*n* = 4; supplementary material, table S1 in appendix S1).

2.5 Results

The restricted dataset that we used for body lipid analyses contained detailed information for 905 humpback whales and 1961 sperm whales (table 2.1). Of the humpback whales, 39.6% were adult males (*n* = 358), 24.1% were non-pregnant females (*n* = 218), 8.1% were pregnant females (*n* = 73), and 28.3% were immature whales (*n* = 256). All the sperm whales were adult males (*n* = 1961) (table 2.1).

Table 2.1. Mean and standard deviation length, total body lipid and energy stores of whales processed at Cheynes Beach Whaling Station for 1953 - 1963 (the following data were excluded from the analysis: humpback whale data from 1952, 1954, 1963 and May; sperm whale data from 1955).

	Humpback whales				Sperm whales			
Reproductive group	**n**	**Length (m)**	**Total Body Lipid (kl)**	**Energy storage (kl/m)**	**n**	**Length (m)**	**Total Body Lipid (kl)**	**Energy storage (kl/m)**
Males	358	12.08 ± 0.62	7.58 ± 1.26	0.63 ± 0.08	1961	13.27 ± 1.22	6.63 ± 1.63	0.49 ± 0.08
Non-pregnant females	218	12.76 ± 0.75	8.71 ± 1.64	0.68 ± 0.11	NA	NA	NA	NA
Pregnant females	73	13.07 ± 0.76	11.30 ± 2.63	0.86 ± 0.16	NA	NA	NA	NA
Immature	256	10.94 ± 0.43	6.38 ± 0.96	0.58 ± 0.08				
Total	905	12.00 ± 0.97	7.81 ± 1.97	0.65 ± 0.12				

Whales in the smaller size classes of both species were under-represented in the data set as 10.7 m (35 ft) was the minimum catch length set by the International Whaling Commission (IWC), the regulatory body for the commercial whaling industry (IWC, 1950).

2.5.1 Inter-species differences

The top-ranked model included both species and length with no interaction term (*w*AIC*c* = 0.54) and accounted for 81% of the variance explained (table 2.2). This demonstrated that total body lipid increased with length for both humpback and sperm whale males and the relationships had the same slope. Length (with the random factor year) accounted for 43% of the variation in body lipid; and the addition of species accounted for an additional 38% of the variation in body lipid (table 2.2). The relationship between body lipid and length for male humpback (y = 1.28x - 7.88) and sperm whales (y = 1.28x - 10.37) demonstrated that, for a given length, male humpback whales stored an average of 2.49 kl (15.6 barrels) (31.9-74.9%) more body lipid than male sperm whales (figure 2.3).

Table 2.2. Ranked (by AIC*c*) linear mixed-effects models investigating the relationship between total body lipid and the explanatory fixed effects; species and length and the random effect of year. Shown are the number of parameters (k), the difference in AIC*c* (Akaike's information criterion corrected for small samples) for each model from the top-ranked model (ΔAICc), the AIC*c* model weight (*w*AIC*c*), the difference in the BIC (Bayesian information criterion) (ΔBIC), the BIC model weight (*w*BIC) and the proportion of variance explained by fixed ($R^2_{GLMM(m)}$) and both fixed and random factors combined ($R^2_{GLMM(c)}$).

Model	*k*	ΔAIC*c*	*w*AIC*c*	ΔBIC	*w*BIC	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
~ species + length + (1|year)	5	0	0.54	0	0.95	0.81	0.81
~ species × length + (1|year)	6	0.33	0.46	5.79	0.05	0.81	0.81
~ length + (1|year)	4	2011.75	<0.01	2006.29	<0.01	0.38	0.43
~ species + (1|year)	4	2697.89	<0.01	2692.43	<0.01	0.11	0.11
~ 1 + (1|year)	3	2875.21	<0.01	2864.30	<0.01	<0.01	0.02

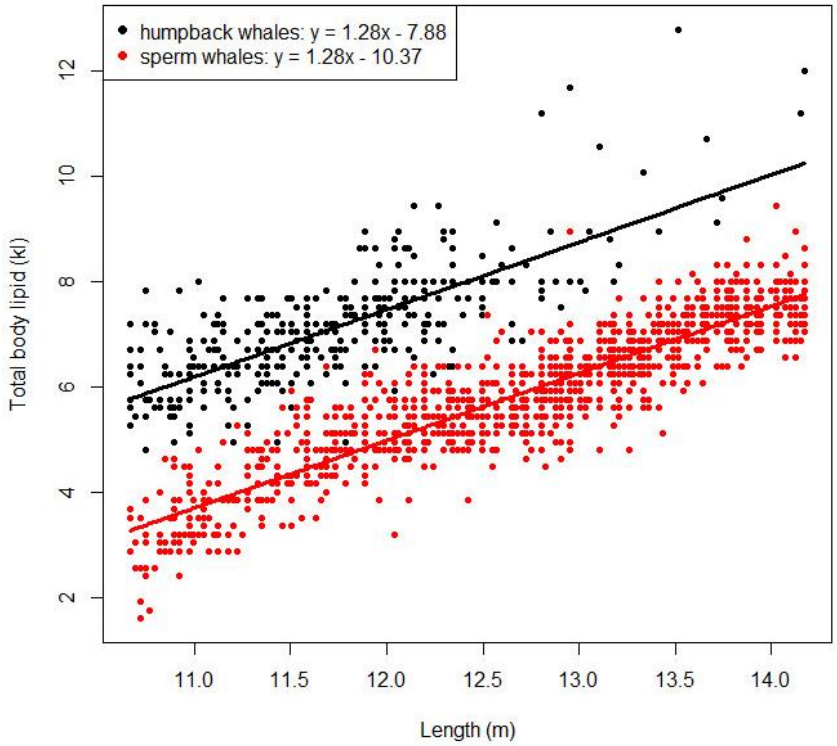

Figure 2.3. Relationship between total body lipid and the predictors in the top-ranked model (length and species) from the suite of models tested to explain total body lipid. Shown are the raw values (sperm whale data were truncated to the maximum length of humpback whales), fitted lines and regression equations of the top-ranked model for each species.

2.5.2 Intra-species differences

2.5.2.1 Humpback whales

The highest ranked model included length and reproductive class and the interaction between them (*w*AIC*c* = 1) (table 2.3), demonstrating that there was a positive relationship between total body lipid and length in all reproductive classes. The slope differed according to reproductive class, with that of the pregnant females being the steepest (y = 2.30x - 18.8), followed by non-pregnant females (y = 1.31x - 7.9) and then males (y = 1.19x - 6.8) (figure 2.4).

Pregnant female humpback whales stored up to twice as much body lipid as other whales of the same body length (figure 2.4), and on average stored 26.2% and 37.4% more body lipid (per metre) than non-pregnant females and mature males, respectively (table 2.1). Immature whales stored, on average, 7.9% and

14.7% less body lipid (per metre) than mature males and non-pregnant females, respectively (table 2.1).

Table 2.3. Ranked (by AIC*c*) linear mixed effects models investigating the relationship between humpback whale total body lipid and the fixed-effects length and reproductive class (class) and the random effect of year**.** Shown are the number of parameters (k), the difference in AIC*c* (Akaike's information criterion corrected for small samples) for each model from the top-ranked model (ΔAICc), the AIC*c* model weight (*w*AIC*c*), the difference in the BIC (Bayesian information criterion) (ΔBIC), the BIC model weight (*w*BIC) and the proportion of variance explained by fixed ($R^2_{GLMM(m)}$) and both fixed and random factors combined ($R^2_{GLMM(c)}$).

Model	*k*	ΔAIC*c*	wAIC*c*	ΔBIC	*w*BIC	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
~ length x class + (1|year)	9	0	1.00	0	1.00	0.69	0.72
~ length + class + (1|year)	7	25.32	<0.01	15.78	<0.01	0.68	0.70
~ length + (1|year)	5	158.42	<0.01	139.32	<0.01	0.59	0.61
~ class + (1|year)	6	860.67	<0.01	846.35	<0.01	0.31	0.32
~ 1 + (1|year)	4	1082.47	<0.01	1058.58	<0.01	<0.01	0.02

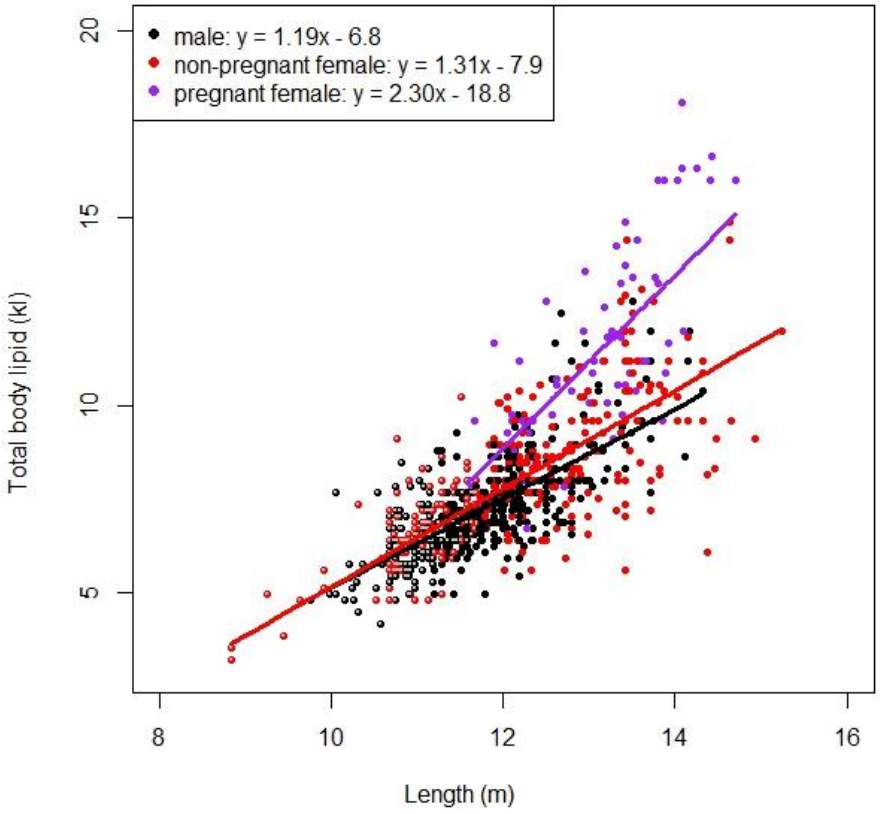

Figure 2.4. Relationship between humpback whale total body lipid and the predictors in the top ranked model (length and reproductive class) from the suite of models tested to explain total body lipid. Shown are the raw values, fitted lines and regression equations for each reproductive class. Immature whales are colour-coded with non-filled centres: immature females with a red outline and immature males with a black outline.

The relationship between body lipid and length of the pregnant females varied according to month (*w*AIC*c* = 0.97) (table 2.4), with those sampled in August having a steeper slope than those sampled in July (figure 2.5). For the males, the model that included the interaction between length and month had equal support (within two AIC points) to the model with length alone when considering AIC*c*; however, the model with length only had complete support when considering the BIC (table 2.4). Thus, there is little evidence for an effect of month. For the non-pregnant females and immature whales, the models that included length and month had majority support when considering AIC*c* (AIC*c* = 0.73 and 0.58, respectively). However, for the former, the BIC selected the model with length only (BIC = 0.85), and for the latter, the BIC values showed equal support for the model length + month (BIC = 0.45) and length only (BIC = 0.51). Thus, there is minor evidence for an effect of month for the immature whales (slightly higher in month 7 (i.e. July)) (supplementary material, figure S2 in appendix S2). The addition of month for all reproductive classes only accounted for an extra 2% of variance explained over and above length (table 2.4).

2.5.2.2 Sperm whales

We did not find any evidence for a seasonal effect on oil yield for the male sperm whales with the model with length only having majority support (wBIC = 0.88) (table 2.5). The relationship between body lipid and length was described by the equation y = 1.23x - 9.8 (figure 2.6). Note that the previous equation provided for sperm whales (figure 2.3) was that for truncated data (to match that of humpbacks in order to meet the assumptions of the model being fitted).

Table 2.4. Ranked (by AIC*c*) linear mixed-effects models investigating the relationship, for each humpback whale reproductive class, between total body lipid and the fixed effects of length and month and the random effect of year. Shown are the number of parameters (k), the difference in AIC*c* (Akaike's information criterion corrected for small samples) for each model from the top-ranked model (ΔAICc), the AIC*c* model weight (*w*AIC*c*), the difference in the BIC (Bayesian information criterion) (ΔBIC), the BIC model weight (*w*BIC) and the proportion of variance explained by fixed ($R^2_{GLMM(m)}$) and both fixed and random factors combined ($R^2_{GLMM(c)}$).

Model	*k*	ΔAIC*c*	*w*AIC*c*	ΔBIC	*w*BIC	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
Males							
~ length x month + (1|year)	9	0	0.48	15.04	<0.01	0.47	0.57
~ length + (1|year)	5	0.13	0.46	0	1.00	0.45	0.55
~ length + month + (1|year)	7	4.23	0.06	11.71	<0.01	0.45	0.55
~ month + (1|year)	6	189.42	<0.01	193.10	<0.01	0.02	0.15
~ 1 + (1|year)	4	197.50	<0.01	193.55	<0.01	<0.01	0.14
Non-pregnant females							
~ length + month + (1|year)	7	0	0.73	3.45	0.15	0.34	0.39
~ length + (1|year)	5	3.07	0.16	0	0.85	0.32	0.36
~ length x month + (1|year)	9	3.72	0.11	13.61	0.01	0.34	0.39
~ 1 + (1|year)	4	58.06	<0.01	51.70	<0.01	<0.01	0.01
~ month + (1|year)	6	60.63	<0.01	60.83	<0.01	<0.01	0.01
Pregnant females							
~ length x month + (1|year)	7	0	0.97	0	0.84	0.55	0.74
~ length + (1|year)	5	7.26	0.03	3.59	0.14	0.53	0.73
~ length + month + (1|year)	6	9.65	0.01	7.85	0.02	0.52	0.71
~ 1 + (1|year)	4	73.34	<0.01	67.73	<0.01	<0.01	<0.01
~ month + (1|year)	5	75.56	<0.01	71.89	<0.01	<0.01	<0.01
Immature							
~ length + month + (1|year)	6	0	0.58	0.25	0.45	0.43	0.50
~ length x month + (1|year)	7	1.27	0.30	4.89	0.04	0.43	0.50
~ length + (1|year)	5	3.15	0.12	0	0.51	0.41	0.48
~ 1 + (1|year)	4	125.38	<0.01	118.82	<0.01	<0.01	0.03
~ month + (1|year)	5	125.33	<0.01	122.38	<0.01	0.02	0.05

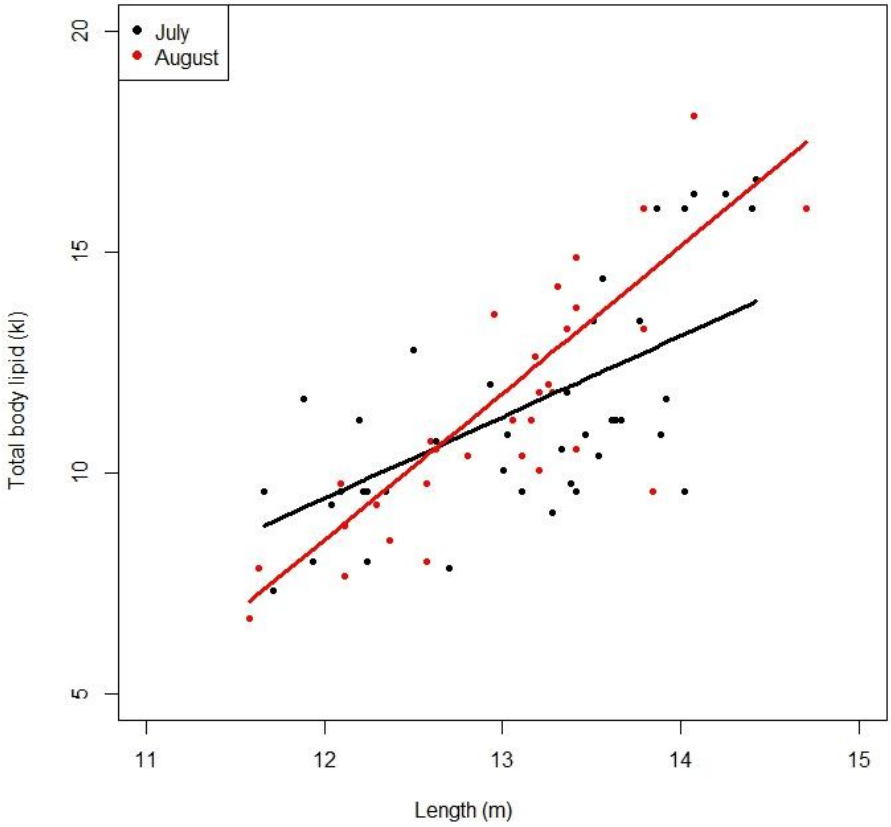

Figure 2.5. Relationship between humpback whale total body lipid and the predictors in the top-ranked model (length and month) from the suite of models tested to explain total body lipid for pregnant females. Shown are the raw values and fitted lines for the pregnant females in the months of July and August.

Table 2.5. Ranked (by AIC) linear mixed-effects models investigating the relationships between total body lipid of male sperm whales and the fixed effects of length and season and the random effect of year. Shown are the number of parameters (k), the difference in AIC*c* (Akaike's information criterion corrected for small samples) for each model from the top-ranked model (ΔAICc), the AIC*c* model weight (*w*AIC*c*), the difference in the BIC (Bayesian information criterion) (ΔBIC), the BIC model weight (*w*BIC) and the proportion of variance explained by fixed ($R^2_{GLMM(m)}$) and both fixed and random factors combined ($R^2_{GLMM(c)}$).

Model	*k*	ΔAIC*c*	*w*AIC*c*	ΔBIC	*w*BIC	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
~ length × season + (1|year)	10	0	1.00	4.25	0.10	0.86	0.86
~ length + season + (1|year)	7	20.74	<0.01	8.30	0.01	0.85	0.85
~ length + (1|year)	4	29.14	<0.01	0	0.88	0.85	0.85
~ season + (1|year)	6	3754.91	<0.01	3736.91	<0.01	0.02	0.02
~ 1 + (1|year)	3	3785.29	<0.01	3750.57	<0.01	<0.01	<0.01

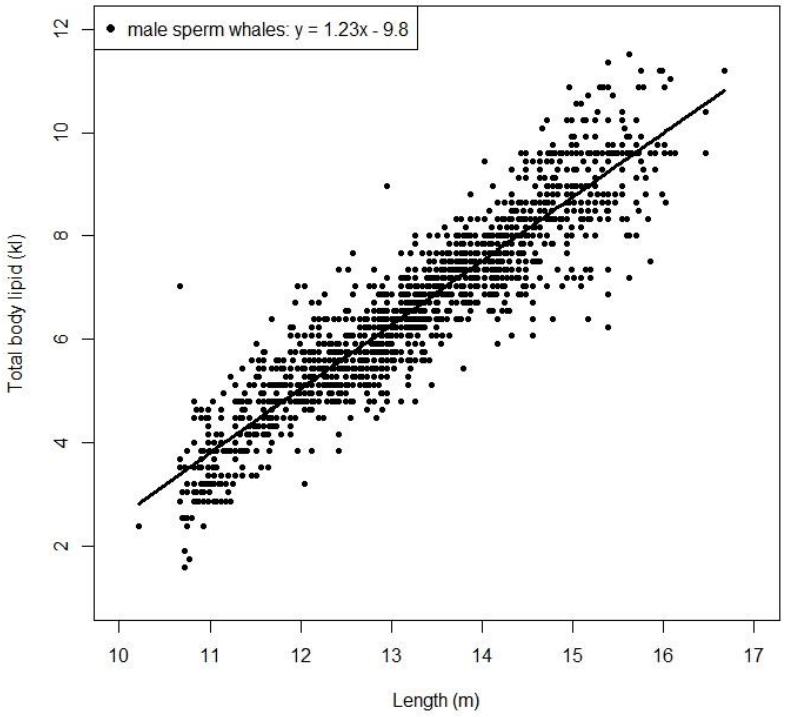

Figure 2.6. Relationship between sperm whale total body lipid (males only) and length (the top-ranked model from the suite of models tested to explain total body lipid). Shown are the raw values, fitted line and regression equation. Note: the equation provided here is slightly different to that provided for sperm whales in Figure 2.3 as here the data were not truncated.

2.6 Discussion

Capital breeders are hypothesised to have higher energy stores than income breeders. Here, we found that capital breeding humpback whales stored 2.49 kl (31.9 - 74.9%) more body lipid than income breeding sperm whales of equivalent length. This not only demonstrates the substantial energy storage requirements of capital breeders, but also provides the first quantification of the energy required for male humpback whales to migrate to the coast of Australia from Antarctica. We also quantified, for the first time, the large lipid storage requirements of breeding female humpback whales and demonstrated that those arriving along the Australian coast later in the season had larger lipid stores than those that arrived earlier. We suggest that this is the result of

delaying migration to maximise energy stores, by increasing time in the Antarctic foraging grounds (Chittleborough, 1965, Dawbin, 1966). Importantly, we developed equations describing the relationship between body lipid and length that can be used both for bioenergetics modelling (e.g. Christiansen et al., 2013a, 2013b, Villegas-Amtmann et al., 2015) and for predicting body lipid in the extensive historical whaling data sets held by the IWC (Allison, 2013), which typically include data on length and sex but not body lipid.

2.6.1 Inter-species comparisons

The difference of 2.49 kl of body lipid that we found between male humpback and sperm whales was constant, regardless of body length, indicating that the total energy required during the breeding fast is the same for individuals of all sizes. Consistent with the theory of mass-specific metabolism (Brodie, 1975), this demonstrates that the relative energy required for migration is greater for smaller individuals than larger individuals.

As the energy stores of the BSD humpback whales decline through the breeding season (Chittleborough, 1965), and those of sperm whales are stable throughout the year (table 2.5), the body lipid difference we found between the two species (2.49 kl) is probably an underestimate of the difference that would be expected when the humpbacks depart their feeding grounds, carrying maximum energy stores. More specifically, the sampling location (Cheynes Beach Whaling Station) is located approximately 3000 km north of the BSD feeding grounds (Chittleborough, 1965) and, contrary to that observed in some other humpback whale populations (Stamation et al., 2007), there is no evidence of feeding during migration. Thus, the energy difference at the beginning of the migration would be expected to decrease continually throughout the season (Chittleborough, 1965), until the humpback whales return to their feeding grounds and resume foraging. We suggest that by the time the humpback whales return to their Antarctic feeding grounds the body

lipid difference between humpback and sperm whales may be much smaller than 2.49 kl and possibly even close to zero. Unfortunately, it was not possible to investigate the energy stores of humpback whales on the return journey to their feeding grounds, as they do not pass Cheynes Beach Whaling Station on their southward migration, and oil yields of individual whales were not recorded at the other whaling stations along the Western Australian coast (Chittleborough, 1965).

We can, however, estimate the maximum energy stores of humpback whales by using information from the Antarctic feeding grounds. Ash (1957) reported that humpback whales accumulate 200 l (1.25 barrels) of body lipid each week in the feeding grounds, and by mid-February (the last sampling date) humpback whales of average length 12.8 m (42 ft) stored an average of 6.77 kl (42.3 barrels) of body lipid. Although departure dates from the feeding grounds are not well known, humpback whales are believed to begin departing in mid-late April (Dawbin, 1966) through to May (Allison, 2013). Accumulating body lipid at a rate of 200 l / week (1.25 barrels / week) (Ash, 1957), a 12.8 m (42 ft) humpback would store between 8.57 and 8.97 kl (53.5 - 56 barrels) of lipid by mid - late April. This compares with 8.43 kl (52.7 barrels) for a male humpback whale of the same size, sampled at Cheynes Beach between June and August (using the equation we developed for male humpback whales; $y = 1.19x - 6.8$). This indicates that the maximum difference in lipid storage between humpback and sperm whales could be 0.14 - 0.54 kl higher (per individual) than the 2.49 kl measured at Cheynes Beach Whaling Station, with the total difference between sperm and humpback whales being potentially as high as 3.03 kl. Although an interesting comparison, these figures must be interpreted with caution due to potential differences in factory efficiencies (Chittleborough, 1965). In addition, no information was provided by Ash about the sex of the whales processed in the Antarctic, or the variation in oil yield according to body length. Regardless of this, our study indicates that the energy required for the annual humpback whale migration is likely to be derived from at least 2.49 kl of body lipid.

In addition to sampling location, we must also account for differences in morphology between sperm and humpback whales, such as the oil-filled spermaceti organ of the sperm whale, which is not believed to play a role in energy storage (Clarke, 1970, Morris, 1975, Clarke, 1978). Given that the sperm whale oil yield records from Cheynes Beach Whaling Station included spermaceti oil as well as sperm oil from the body (Frost, 1978), and that an average of 11% of the total oil produced from a sperm whale is spermaceti oil (Clarke, 1978), the difference of 2.49 kl (15.6 barrels) of body lipid that we found between humpback and sperm whales is probably an underestimate of the difference in body lipid that is stored for energy utilisation.

Interpreting differences in lipid stores between mysticetes and odontocetes, in terms of energetics, is a complex task due to differences in life history, behaviour, morphology and lipid storage patterns. For example, humpback whales are a baleen whale specialised for long-distance migration. They have thick blubber that plays a role in thermoregulation, but is primarily an energy storage depot (Slijper, 1962, Lockyer, 1991). Sperm whales, by contrast, are specialised for deep diving. They have large heads that can weigh over one-third of their total body weight (Clarke, 1978) and thick blubber that plays a role in structural support, thermoregulation and energy storage (Lockyer, 1991). Previous comparisons between baleen whales and sperm whales have been based on body and tissue weights (Lockyer, 1976, 1991), and have demonstrated differences between slow-swimming baleen whales (humpback and North Pacific right whales (*Eubalaena glacialis*)), fast-swimming baleen whales (blue, fin, sei (*Balaenoptera borealis*) and Bryde's (*Balaenoptera edeni*)) and sperm whales; more specifically, that: i) the slow-swimming baleen whales are heavier per unit body length than sperm whales, while the fast-swimming baleen whales are lighter (Lockyer, 1976); ii) right whales contained greater proportions of blubber than sperm whales, while the fast swimming baleen whales contained less (Lockyer, 1976, 1991) (unfortunately, no information was available for humpback whale blubber); iii) the fast-swimming baleen whales

have a higher proportion of muscle than sperm whales (Lockyer, 1976, 1991) and store the majority of their lipid stores in their muscle (Lockyer, 1981b). Sperm whales, in comparison, store almost no lipid in their muscle (Lockyer, 1991).

Measurement of total body lipid provides a useful method of comparing energy stores between species, as it enables inclusion of energy stores from all lipid depots, regardless of their function or storage capacity. Although this information is very valuable, there are some limitations of historical whaling data that need to be recognised: i) the oil extracted from each whale is dependent on factory efficiency (Chittleborough, 1965); ii) size classes and reproductive classes were not all equally represented as the whaling industry operated under regulations which included a minimum catch size of 10.7 m (35 ft) for humpback and sperm whales, and which also prohibited the taking of any calves and accompanying (lactating) females (IWC, 1950); and iii) at times, lengths of undersized whales were falsified to avoid infraction reports (Chittleborough, 1965, Clapham and Ivashchenko, 2016). Despite these limitations, however, the catch records from Cheynes Beach Whaling Station provide an extremely valuable source of information on energy storage in cetaceans as they provide a measure of total body lipid for a large number of individual whales. Large, detailed datasets such as this are exceptionally rare, and cannot be replicated in the modern era.

2.6.2 Intra-species comparisons

2.6.2.1 Sperm whales

Sperm whales are income breeders that accrue regular energetic 'income' (Bannister, 1968, 2008) and adjust their foraging rate according to energy demands (Lockyer, 2007). The energy stores of the male sperm whales in this study were fairly consistent throughout the year, indicating that there was adequate food supply to satisfy their energetic demands year-round. There was

no evidence of seasonal energy storage such as that found in other income breeders like long-finned pilot whales (*Globicephala melas*), which store energy in winter for use in reproduction during spring and summer (Lockyer, 1993).

Sperm whale weight, girth and blubber thickness have all been shown to increase with body length (Gambell, 1972, Lockyer, 1976, Lockyer, 1981a, Lockyer, 1991). However the relationship between blubber thickness and body length has at times been confounded by high individual variability and small sample size (Evans et al., 2003). This study confirmed the high individual variability in energy stores found in the Evans study (Evans et al., 2003), but the extensive nature of the dataset (1961 males) and the large range of body lengths (10.2 m (33.5 ft) - 16.8 m (55 ft)) facilitated the identification of a positive relationship for the males. The lack of small whales in this study (no whales less than 10.2 m (33.5 ft)) places some uncertainty around the validity of the equation for the relationship between lipid and length for smaller individuals. However, the girth - length relationship of Lockyer (Lockyer, 1991) included smaller individuals (3.7 m (12 ft) in length) and suggests that this relationship is valid for all size classes.

2.6.2.2 Humpback whales

Baleen whale energy stores have been shown to vary according to reproductive status (Chittleborough, 1965, Lockyer, 1981b, 1986, 1987, Perryman and Lynn, 2002, Miller et al., 2012) with pregnant blue and fin whales accumulating 20 - 25% more lipid than resting females (i.e. those not pregnant or lactating) (Lockyer, 1981b), to satisfy the high energy demands of gestation and lactation (Lockyer, 1981b, Oftedal, 1997). Consistent with this, pregnant female humpback whales in this study stored an average of 26.2% and 37.4% more body lipid than non-pregnant females and males, respectively. Interestingly, our body lipid - length equations illustrate that the longer pregnant females stored relatively more energy than the shorter pregnant females, thus having

more energy to transfer to their offspring (Oftedal, 1997). Maximising energy stores is critical for capital breeders, who must trade off their own body condition to maximise offspring survival (Bradford et al., 2012, Christiansen et al., 2014b). Maternal energy stores have been shown to influence fecundity (Williams et al., 2013), foetal growth (Christiansen et al., 2014b), weaning mass (Arnbom et al., 1993, Wheatley et al., 2006), and, thus, ultimately survival (McMahon et al., 2000, Wheatley et al., 2006). Large maternal energy stores enable longer fasting periods for the mothers (Lindstedt and Boyce, 1985, Millar and Hickling, 1990), which in turn provide calves with a thermoregulatory benefit of longer duration in the warm waters of their breeding areas (Brodie, 1975). The relatively low energy stores of the smaller pregnant females in this study suggest that they will be more vulnerable to nutritional stress during the migration fast, particularly after commencing lactation (Lockyer, 1984), and will probably produce smaller calves with lower survival rates.

HYPOTHESIS I): MATURE, NON-PREGNANT FEMALES WILL HAVE VARIABLE ENERGY STORES DUE TO THEIR VARYING REPRODUCTIVE STATES.

As expected, the relative energy stores of the mature non-pregnant females exhibited high variation, due to their different reproductive states (Lockyer, 1981b, Perryman and Lynn, 2002, Miller et al., 2011, Bradford et al., 2012, Miller et al., 2012). Females in this study presumably include individuals preparing for pregnancy, resting females and those that had recently terminated lactation. Lactating females generally have the lowest energy stores in the population (Lockyer, 1981b, Perryman and Lynn, 2002, Bradford et al., 2012, Miller et al., 2012), while those preparing for pregnancy tend to have the highest (Miller et al., 2011). Although whaling industry regulations restricted the capture of lactating females accompanying calves (IWC, 1950) (thus preventing inclusion in this dataset), females with weaned calves were allowed to be captured. Given that lactation is generally terminated at the end of June (Chittleborough, 1958), females that recently terminated lactation may have been caught during July and August and thus included in this study.

HYPOTHESIS II): MATURE MALES WILL HAVE HIGHER ENERGY STORES THAN MATURE NON-PREGNANT FEMALES, DUE TO THEIR NEED TO COMPETE FOR, AND ACCESS, BREEDING FEMALES.

The relative energy stores of the males were similar to those of the non-pregnant females, suggesting that their energy demands over the breeding season are also similar. Contrary to our expectations, there was no evidence to suggest that the males stored higher energy reserves than females to fuel the competitive behaviours observed in the breeding grounds (Baker and Herman, 1984, Spitz et al., 2002). Male energy stores may be driven by a trade-off between energy accumulation in the feeding grounds and time maximisation, and hence mating opportunities, in the breeding grounds (Craig et al., 2003). It has been shown in other migratory species, that males in good condition that reach the breeding grounds first have higher rates of breeding success (Marra et al., 1998, Smith and Moore, 2005). Thus, the decision for male humpback whales to depart the feeding grounds may be based on maximising energy stores in a given time-frame, rather than maximising energy stores to a physiological limit, at the cost of extending time in the feeding grounds.

HYPOTHESIS III): IMMATURE WHALES WILL HAVE HIGHER ENERGY STORES THAN MATURE MALES AND MATURE NON-PREGNANT FEMALES DUE TO THE HIGH ENERGY DEMANDS OF GROWTH.

It is generally accepted that immature mammals, including baleen whales, have greater energy demands than adults due to the energetic costs of body growth (Brody, 1945, Worthy, 1987, Fortune et al., 2013) and high mass-specific metabolic demands (Costa, 1993). The relatively low energy stores of the immature whales in this study, in comparison with all other reproductive classes, suggest that they will be more prone to nutritional stress during the migration fast than mature whales. This appears to be supported by stranding data from the BSD population, which show that the majority of strandings along the migratory corridor are immature whales in generally poor body condition (Coughran et al., 2013).

HYPOTHESIS IV): INDIVIDUALS SAMPLED AT CHEYNES BEACH WHALING STATION LATER IN THE SEASON WILL HAVE HIGHER ENERGY STORES THAN THOSE SAMPLED EARLIER, AS THEY SPEND THE SUMMER ACCUMULATING AND STORING ENERGY AT A RATE OF 200 L / WEEK, AND ALL MIGRATE AT THE SAME SPEED.

To gain a complete understanding of the effect of sampling date on energy stores, we must take into account reproductive status, as it is thought to influence residency times in the Antarctic foraging grounds (Chittleborough, 1965, Dawbin, 1966, Dawbin, 1997), and thus drive the temporally staggered migration observed in humpback whale populations around the globe (Chittleborough, 1965, Dawbin, 1997, Craig et al., 2003). Our current understanding is that lactating females reside in the foraging grounds for approximately 4.5 months; immature animals, mature non-pregnant females and mature males stay for approximately 5.5 months; and pregnant females remain for about 6.5 months (Dawbin, 1966).

Our investigations of temporal differences in body lipid within each reproductive group provide evidence of individual variation in residency times in the feeding grounds coupled with an effect on energy stores. In particular, pregnant females sampled at Cheynes Beach Whaling Station later in the season had higher energy stores, on average, than those sampled earlier. As there is no evidence of differences in migration speed (Dawbin, 1997), arrival date along the Australian coast appears to reflect the departure date from the Antarctic, which in turn reflects residency times in the feeding grounds. Given that humpback whales accrue 200 l of body lipid per week in the feeding grounds (Ash, 1957), and it takes approximately three months for the entire migratory stream to pass Cheynes Beach Whaling Station *en route* to the breeding grounds (Chittleborough, 1965), an increase in energy stores with sampling date is perhaps not surprising. Such an increase, however, has not been documented previously, and is the opposite of what may typically be expected in a capital breeding population. For example, Chittleborough (1965) demonstrated that lipid stores of the BSD humpback whale population decreased during the

breeding season, by sampling the population at a fixed point (Carnarvon Whaling Station: 24° 53'S, 113° 38'E; ~1100 km north of Cheynes Beach Whaling Station) during two different stages of the migration (northbound and southbound). This sampling regime described variation in energy stores *between* the northbound and southbound migratory streams that resulted from an estimated six-week difference in fasting duration (Dawbin, 1997, Jenner et al., 2001), plus variation *within* the migratory streams due to variable residency times in the Antarctic feeding grounds. In contrast, our sampling regime describes variation in energy stores *within* the northbound migratory stream that are due solely to varying residency times in the Antarctic foraging grounds. Understanding the differences between these two sampling regimes is crucial, as they have significant effects on the results and thus on our interpretation of energy store variation during the breeding season.

Interestingly, our finding of an energetic benefit (for the pregnant females) from extra time in the feeding grounds appears to be restricted to the larger (longer) individuals. The relatively low body lipid stores of the smaller (shorter) pregnant females sampled later in the season may demonstrate their inferior energy storage capabilities due to small body size, size-related foraging efficiency (Goldbogen et al., 2010) or perhaps late arrival in the feeding grounds. Given that small body size appears to increase vulnerability to nutritional stress during the migration fast (e.g. Coughran et al., 2013), the additional energetic demands of reproduction (Lockyer, 1981b) most likely renders the smaller breeding females (and their calves) as the most vulnerable component of the population during the annual migration.

2.7 Conclusion

The unique data summarised here demonstrate that capital breeding humpback whales store substantially more body lipid than income breeding sperm whales to fuel their annual migration, and that the energy stores of capital breeders are

driven by a combination of body size, reproductive status and time spent in the feeding grounds. Pregnant female humpback whales delay their departure from the feeding grounds to maximise energy stores and satisfy the high costs of gestation and lactation. The smaller pregnant females, however, do not accumulate as much energy as the larger females, and are thus more vulnerable to nutritional stress during migration. Our study has provided new insights into the life-history strategies of large cetaceans, and the relationships we have quantified will be useful in developing ecosystem and bioenergetics models, and in understanding the potential impacts of environmental change. Moreover, the data we present here are particularly important given that such a large and detailed dataset on cetacean energy stores will probably never be collected again.

2.8 Acknowledgements

We are grateful to the Cape Conservation Group (Exmouth) for introducing us to B. Teede whom we are indebted to for showing us the humpback whale catch records from the NorWest Whaling Company and providing valuable information about the commercial whaling era. Without this, the data used in this research would remain hidden away in the historical archives. We thank J. Bannister for providing catch records and other information about sperm whales. This research was only possible due to the dedicated early work of J. Bannister and the late G. Chittleborough.

2.9 Supplementary material

2.9.1 Appendix S1: Supplementary data

Table S1. Body lengths of whales processed at Cheynes Beach Whaling Station (1952-1963). Number and total body length (mean and SD) of humpback and sperm whales processed at Cheynes Beach Whaling Station, shown each year and each month between 1952 and 1963. F = females.

		Humpback whales (m)												Sperm whales (m)											
		Reproductive group												Reproductive group											
		All whales			Males			Pregnant F			Non pregnant F			All whales			Males			Pregnant F			Non pregnant F		
		n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd
Year	1952	48	12.79	0.75	24	12.38	0.71	8	13.14	0.40	16	13.24	0.60	0			0			0			0		
	1953	75	12.23	1.10	41	12.07	0.94	12	13.23	0.46	22	11.96	1.35	0			0			0			0		
	1954	3	12.04	1.80	2	11.05	0.75	0			1	14.02		0			0			0			0		
	1955	122	12.24	1.06	78	12.14	0.79	3	12.60	0.93	41	12.42	1.45	5	14.05	2.52	4	14.88	1.97	0			1	10.74	
	1956	119	12.27	1.03	58	11.73	0.73	14	13.18	0.81	47	12.66	1.04	61	13.65	1.22	61	13.65	1.22	0			0		
	1957	101	12.05	0.83	58	11.81	0.65	13	13.00	0.93	30	12.11	0.84	139	13.06	1.56	122	13.36	1.41	4	10.75	0.03	13	10.89	0.26
	1958	82	11.81	0.89	36	11.45	0.68	4	12.95	0.96	42	12.00	0.91	258	12.97	1.37	228	13.25	1.19	3	10.37	0.54	27	10.89	0.14
	1959	159	12.08	1.02	75	11.80	0.85	21	13.11	0.72	63	12.07	1.08	137	13.41	1.30	137	13.41	1.30	0			0		
	1960	105	11.74	0.84	62	11.50	0.66	3	12.82	1.13	40	12.02	0.93	282	13.08	1.33	273	13.15	1.29	1	10.67		8	10.88	0.20
	1961	105	11.57	0.78	53	11.39	0.61	0			52	11.74	0.89	454	13.25	1.15	450	13.27	1.13	2	11.15	0.61	2	10.49	0.39
	1962	40	11.77	0.72	25	11.66	0.61	3	12.83	0.90	12	11.74	0.74	568	13.21	1.21	556	13.26	1.17	0			12	10.83	0.46
	1963	2	11.93	0.48	0			0			2	11.93	0.48	135	13.15	1.23	134	13.16	1.23	1	11.20		0		
	Total	961			512			81			368			2039			1965			11			63		
Month	1	0			0			0			0			29	12.62	1.41	24	13.02	1.20	2	10.68	0.02	3	10.74	0.03
	2	0			0			0			0			1	12.09	0.00	1	12.09		0			0		
	3	0			0			0			0			111	13.08	1.19	108	13.14	1.15	0			3	11.09	0.51
	4	0			0			0			0			245	12.98	1.30	237	13.05	1.26	0			8	10.83	0.16
	5	3	11.36	1.37	1	10.80		0			2	11.65	1.81	205	12.94	1.29	186	13.14	1.19	3	11.15	0.46	16	10.99	0.24
	6	257	11.85	1.08	120	11.53	0.72	2	13.18	1.29	135	12.12	1.25	95	12.97	1.28	90	13.10	1.19	0			5	10.65	0.34
	7	574	12.01	0.92	330	11.78	0.78	44	13.12	0.77	200	12.15	0.97	61	13.09	1.12	60	13.14	1.07	0			1	10.29	
	8	127	12.54	0.83	61	12.29	0.69	35	13.02	0.68	31	12.48	1.01	222	13.13	1.17	217	13.19	1.13	0			5	10.85	0.05
	9	0			0	0		0			0			335	13.42	1.27	330	13.46	1.24	1	10.72		4	10.73	0.35
	10	0			0	0		0			0			346	13.26	1.27	342	13.29	1.25	1	10.80		3	10.75	0.05
	11	0			0	0		0			0			301	13.36	1.34	284	13.52	1.22	4	10.49	0.49	13	10.92	0.24
	12	0			0	0		0			0			88	13.20	1.28	86	13.25	1.23	0			2	10.72	0.04
	Total	961			512			81			368			2039			1965			11			63		

2.9.2 Appendix S2: Supplementary analyses

This appendix contains the following supplementary figures:

Figure S1. Frequency distribution of total body length of humpback and sperm whales sampled at Cheynes Beach Whaling Station between 1952 and 1963.

Figure S2. Relationship between humpback whale total body lipid and the predictors, length and month.

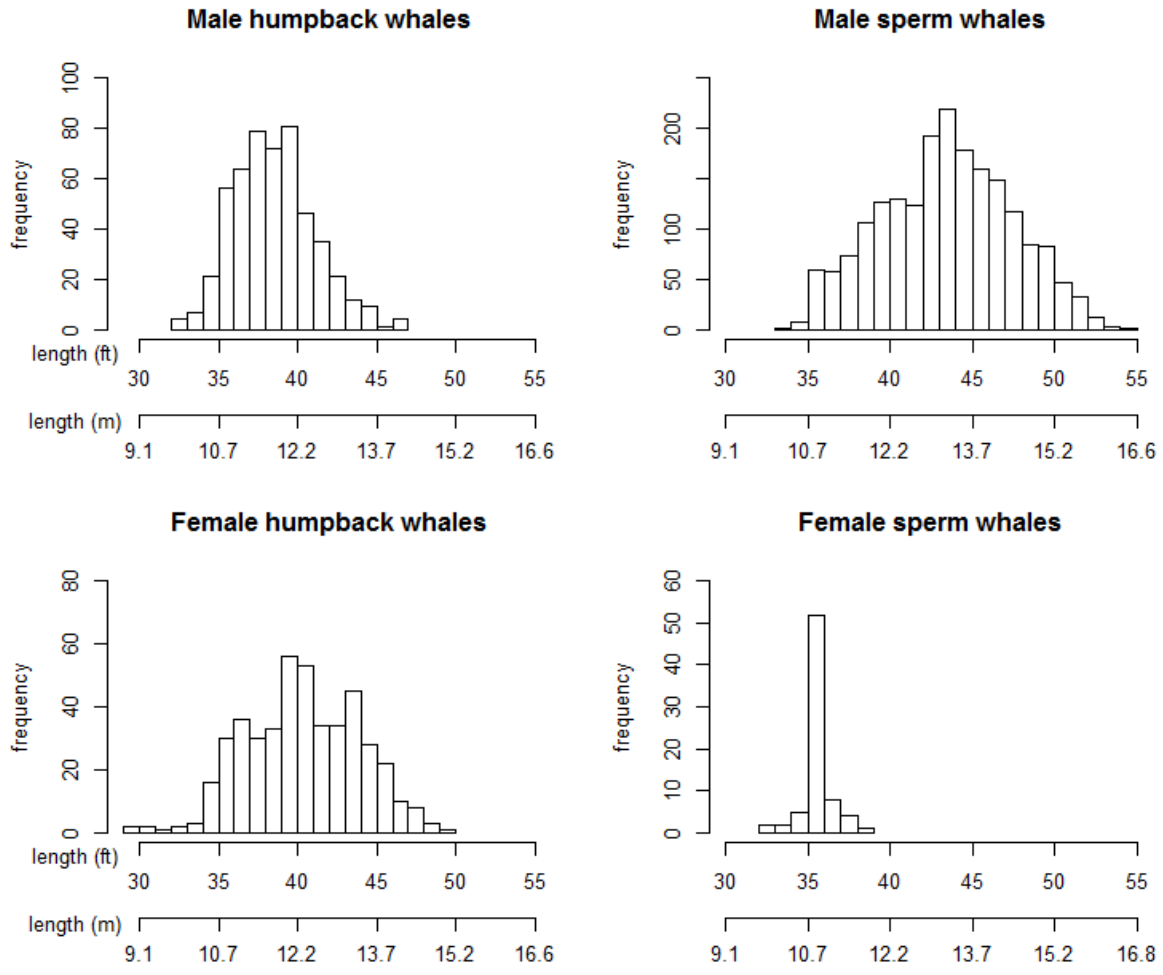

Figure S1. Frequency distribution of total body length of humpback and sperm whales sampled at Cheynes Beach Whaling Station between 1952 and 1963. The two x axes for each plot illustrate length in two different scales: top axis - as originally measured (ft); bottom axis - after conversion into SI units (m).

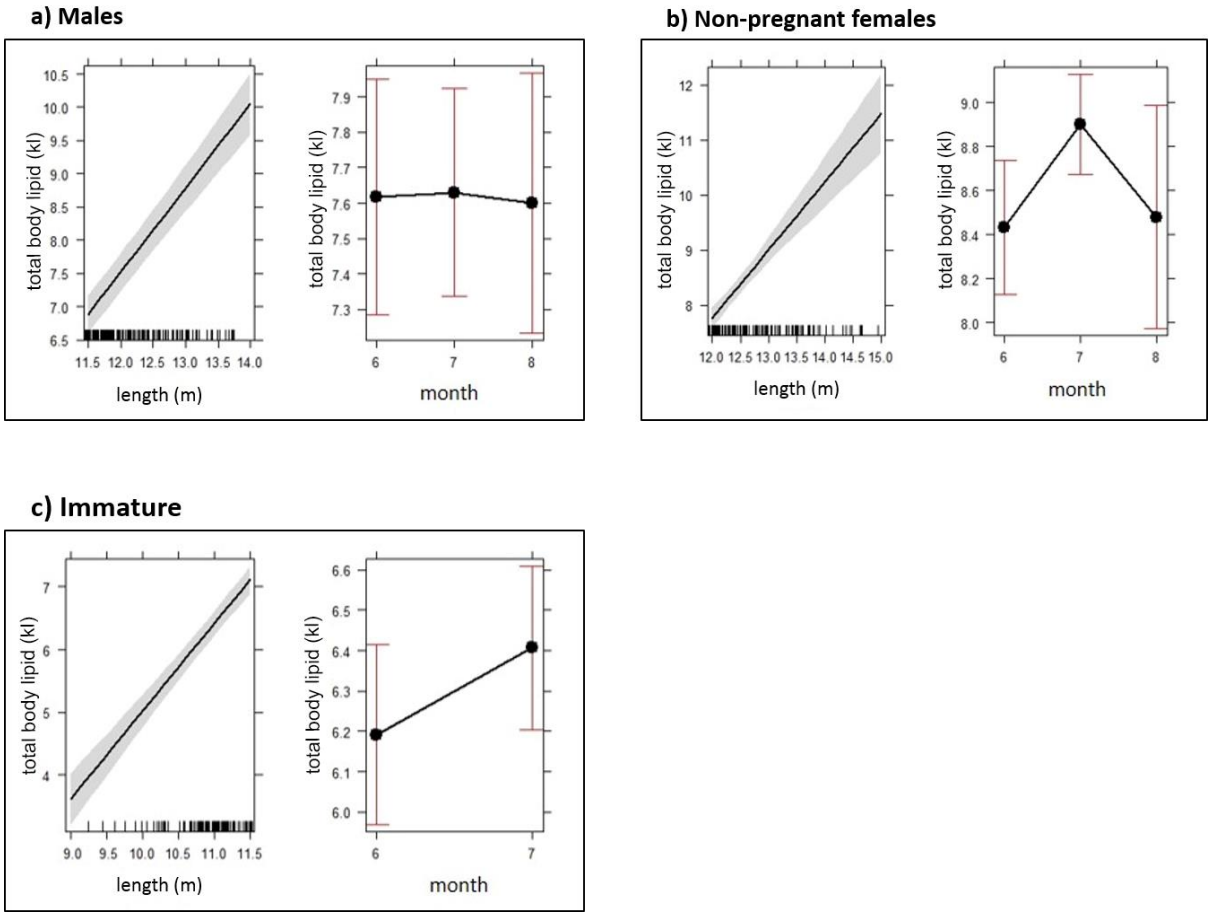

Figure S2. Relationship between humpback whale total body lipid and the predictors (length and month) for a) males; b) non-pregnant females; and c) immature individuals. The shaded areas represent the 95% confidence interval; the error bars represent standard error.

Chapter 3

Annual differences in cow body condition loss and calf growth during lactation in the capital breeding humpback whale

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3.1 Abstract

Lactation is the most energy demanding activity in the mammalian lifecycle. Capital breeders such as humpback whales (*Megaptera novaeangliae*) fuel lactation entirely by endogenous energy reserves whilst nursing their calves in non-productive breeding grounds. Although critical for calf growth and survival, very little is known about the costs of lactation and maternal investment in humpback whales. We collected vertical aerial photographs of lactating humpback whales and dependent calves at different stages of their reproductive cycle, within and between seasons, to investigate maternal investment and whether this varied between years. We measured a cross-sectional subsample of the population as repeated measurements of the same individuals over time were not possible. Using photogrammetric methods, we determined that width measurements at 50% and 70% body length were the most useful locations for estimating body condition of lactating cows and calves, respectively. The width of the lactating females decreased at mean rate of 0.36 and 0.65 cm/day during early lactation in 2013 and 2015, respectively, while they were simultaneously fasting and lactating. This rate decreased to 0.14 cm/day during late lactation when a period in the feeding grounds presumably supplemented maternal energy reserves. Calf body length increased at a mean rate of 3.1 and 2.4 cm/day in 2013 and 2015, respectively, during early development and 0.68 cm/day in the latter stages. The growth pattern of the calves appeared to be one of rapid length increase during the early stages of development (from birth to ~6 weeks) and body condition increase in the latter stages of development (after ~6 weeks of age). The annual differences in cow body condition decline and calf growth may have been caused by differences in energy expenditure in the breeding grounds or by differences in maternal energy stores. Our results will help to better understand maternal investment in humpback whales and establish a baseline of humpback whale condition that can be used to investigate how individual whales and their populations respond to environmental change.

3.2 Introduction

As the world goes through a period of rapid climate change (IPCC, 2007, 2014), understanding the effects of environmental change on biological organisms will be essential for conservation purposes (e.g. Burek et al., 2008). Health indices, such as body condition or bacterial biomes, that describe fitness or resilience, are valuable tools for assessing such relationships (Bossart, 2011, Apprill et al., 2014, Apprill et al., 2017). Body condition, a measure of an individual's energetic status attained through feeding (Schulte-Hostedde et al., 2001, Peig and Green, 2009), is a particularly useful index, as it provides a strong link between animal fitness and the physical environment.

Capital breeders fuel survival and reproduction with stored energy reserves (Stearns, 1989, Jönsson, 1997), and thus undergo cycles of energy accumulation during intensive feeding periods and energy expenditure during times of food scarcity. Baleen whale body condition thus fluctuates seasonally according to energy storage and utilisation (Lockyer, 1981b), and annually, according to environmentally mediated prey availability in the feeding grounds (Lockyer, 1986, Ichii et al., 1998, Miller et al., 2011). Quantifying these variations over different time scales, and under differing environmental regimes, is essential for understanding individual fitness and how it may respond to a changing climate (e.g. McMahon and Burton, 2005, Harwood et al., 2015, Clausius et al., 2017a).

In mammals, lactation is the most costly activity in the reproductive cycle (Oftedal, 1993). For capital breeding baleen whales, maternal energy stores support a rapid offspring growth rate where calf mass increases more than ten-fold between parturition and weaning (Lockyer, 1981b). Much of this growth is attained while the mother is undergoing a period of simultaneous lactation and fasting (Chittleborough, 1965, Dawbin, 1966, Lockyer, 1981b), and in some cases, also simultaneous gestation (Chittleborough, 1958). This requires pregnant baleen whale females to accumulate

large energy reserves in the Antarctic feeding grounds prior to parturition (Lockyer, 1981b, Irvine et al., 2017b). The size of these maternal energy reserves can influence offspring survival through the effects on energy transfer and thus early growth and development (Wheatley et al., 2006).

Despite the importance of early development on life-long fitness (Lindström, 1999) and the extreme energetic demands of simultaneous lactation and fasting (Oftedal, 1993, 2000), very little is known about maternal energy expenditure and calf growth rates in the breeding grounds, and how these may vary each year. For humpback whales, seasonal body condition loss and calf growth have been quantified for mothers and post-neonate calves over a 31 day period during the southern migration (Christiansen et al., 2016). However, the growth of neonate calves and the condition of their mothers has not been quantified and variations between years have not been investigated. Our goal in this study was to extend the current knowledge of maternal investment and calf growth by collecting data on body condition and size at two different stages of the migration, and over two separate years, to gain an understanding of both intra- and inter-annual variation.

The largest known population of humpback whales globally, Breeding Stock D (BSD) (Branch, 2011, Salgado Kent et al., 2012, IWC, 2014), breeds in the tropical waters along the western Australian coast. During August, large numbers of lactating females and neonate calves frequent the inshore waters west of North West Cape (22^{o}S) as they migrate northward from their Antarctic feeding grounds (Irvine et al., 2017a). During September and October each year, large numbers of lactating females with older calves rest in the waters east of North West Cape (Exmouth Gulf) as the population makes its return journey southwards to the Antarctic feeding grounds (Jenner et al., 2001, Irvine et al., 2017a). The whales' distribution close to the coast provides easy access to lactating females, and their calves, during both the northern and southern stages of their annual migration.

Body condition in small animals is generally determined by the relationship between body mass and body size (Schulte-Hostedde et al., 2001). For large animals such as whales, however, body condition can be difficult to determine as large body size often prohibits capture for measurement and their completely marine existence makes accessibility challenging. Photogrammetry is a method that does not require close access to animals, can be applied remotely and is capable of capturing detailed information on large numbers of individuals (Bell et al., 1997). In addition, it uses morphometric measurements such as width (a proxy for girth), which is considered to be one of the best methods of estimating cetacean body condition (Rice and Wolman, 1971, Lockyer, 1986, Lockyer, 1987) as it accounts for fat stored in multiple body tissues including the blubber, muscle and viscera (Slijper, 1962, Lockyer, 1981b, Lockyer, 1991). It is thus ideal for cetacean research and has been used successfully to determine the relative body condition of a range of baleen whales, including gray (*Esrichtius robustus*), right (*Eubalaena glacialis* and *E. australis*), humpback and blue (*Balaenoptera musculus*) whales (Perryman and Lynn, 2002, Miller et al., 2012, Christiansen et al., 2016, Durban et al., 2016).

In this study, we used photogrammetric methods on free swimming humpback whales to quantify body condition and size during their annual migration. Our specific objectives were to: (1) investigate the distribution of energy stores along the body to determine which location is the best index of body condition; (2) investigate maternal investment by quantifying intra- and inter-annual changes in body condition of lactating females and growth of dependent calves; and (3) investigate the effect of maternal energy stores on calf development by quantifying the relationship between female body condition and calf body condition and growth. By quantifying intra- and inter-annual body condition on a cross-sectional sample of the population, the ground work for its application to monitoring body condition changes in free-swimming humpback whales under varying climatic regimes has been undertaken.

3.3 Methods

3.3.1 Study site and timing

The study was conducted on lactating female whales and their calves off North West Cape and in Exmouth Gulf, Western Australia (Figure 3.1). These two locations were selected as they enabled sampling of the population at two different stages of the whale's annual migration. Females in the early stages of lactation, and their calves, were sampled along North West Cape during late July and August, which corresponds to the time of peak parturition of the BSD population (Chittleborough, 1958). Females in later stages of lactation, and their calves, were sampled in Exmouth Gulf during September, as they rested during their southern migration (Jenner et al., 2001).

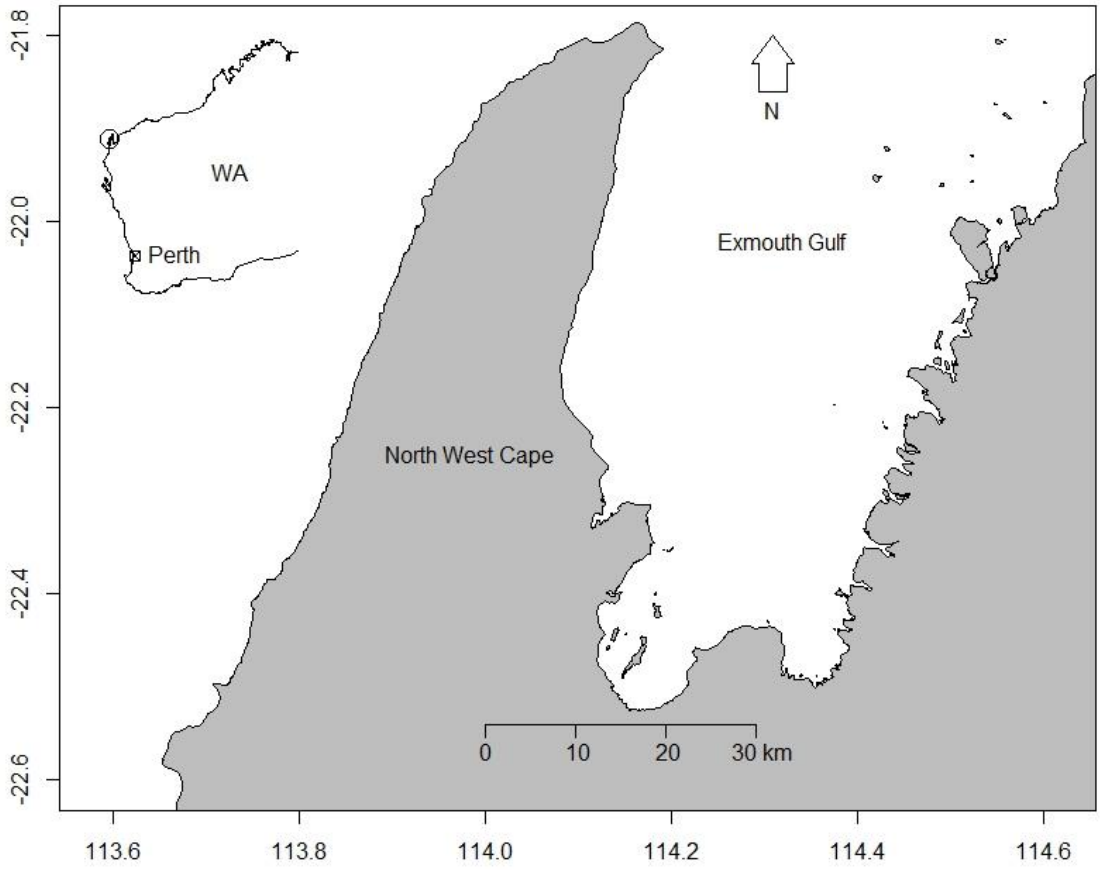

Figure 3.1. Map of the study area of North West Cape and Exmouth Gulf along the north-west coast of Western Australia (WA).

3.3.2 Aerial surveys and data collection

A total of 25 aerial surveys, consisting of two people (pilot and photographer), were flown between July and September in 2013 (n=13) and 2015 (n=12) to collect vertical photographs of humpback whales for photogrammetry. All surveys were conducted at approximately 95 knots (170 km/hr) from a high wing, light aircraft (Cessna 172). Surveys in 2013 were conducted at a height of ~305 m (1000 ft) while those in 2015 were conducted at ~245 m (800 ft). Sampling was carried out according to the description (Figure 4.2 and accompanying text) outlined on p. 89.

Photos were taken using a Canon digital SLR (EOS 50D in 2013; EOS 5D Mark III in 2015) fitted with a Canon 85 mm fixed lens. When a cow-calf pair was identified, the photographer leaned out of the starboard window and took a series of vertical photographs when the aircraft was directly above the whales. A bubble level was attached to the back of the hand-held camera to ensure that the camera was level as each photograph was taken. All cow-calf pairs observed at the surface were photographed and where possible (i.e. when the whales remained at the surface for an extended duration) photos of each pair were taken during three separate passes.

3.3.3 Identification and classification of lactating females and calves

Lactating females and their calves were classified according to colour and size. For each cow-calf pair photographed, the relative size was used to distinguish the females from calves, with all individuals in close association with a larger animal and less than 63% of the length of the accompanying animal (the mother) being classified as calves (Clapham et al., 1999).

Calf colour was described relative to that of the mother (i.e. the closest accompanying adult). As calf colour changes from light grey at birth to the dark grey - black adult colours over the course of about a month (Kaufman and Forestell, 2006), light grey calves were classified as neonates (< 1 month of age) while those

the same colour as their mother were classified as post-neonate (> 1 month of age). Calves that were mid grey were classified according to their proportional size (relative to their mother), with those ≤ 0.42 mother body length being classified as neonates and those > 0.42 mother body length being classified as post-neonates. Calves that were approximately 63% of the larger animal's body length were recognised as being born the previous year and were classified as calves nearing independence (Clapham et al., 1999). The classification of these individuals as calves (nearing independence) was further confirmed by their short relative head size (Lockyer, 1981b) and the poor condition of the accompanying individuals, typical of females after extended periods of energy loss during lactation (Lockyer, 1981b, Perryman and Lynn, 2002, Bradford et al., 2012, Miller et al., 2012).

The lactation stage of the females was classified relative to the developmental stage of their calves. Females accompanying a neonate calf were classified as 'early lactation'; those accompanying a post-neonate calf were classified as 'mid lactation'; those accompanying a near-independent calf were classified as 'late lactation'.

3.3.4 Measurements from aerial photographs

Relative measurements of cows and calves in aerial photographs were made using ADOBE Photoshop Creative Cloud (2015.0.1 Release). As the aircraft was not fitted with a radar altimeter, or other instrumentation capable of accurate altitude measurement, relative (rather than absolute) measurements of whales were taken. This also enabled direct comparison between images taken with different camera body and lens configurations, while still addressing the objectives of this study. The required body dimensions (length and widths) were measured in pixels and then converted into relative body size ratios (widths divided by lengths) as indicators of energy stores along the body. Total body length was defined as the distance between the tip of the rostrum and the tail notch (Figure 3.2). Body width was measured at eight locations along the body, including: i) at increments equivalent to

10% of the total body length, from the anterior (starting at the tip of the rostrum) to the posterior of the animal (at the location corresponding with 80% of the total body; Figure 3.2) following Miller et al. (2012) and ii) between the eyes, according to Christiansen et al. (2016).

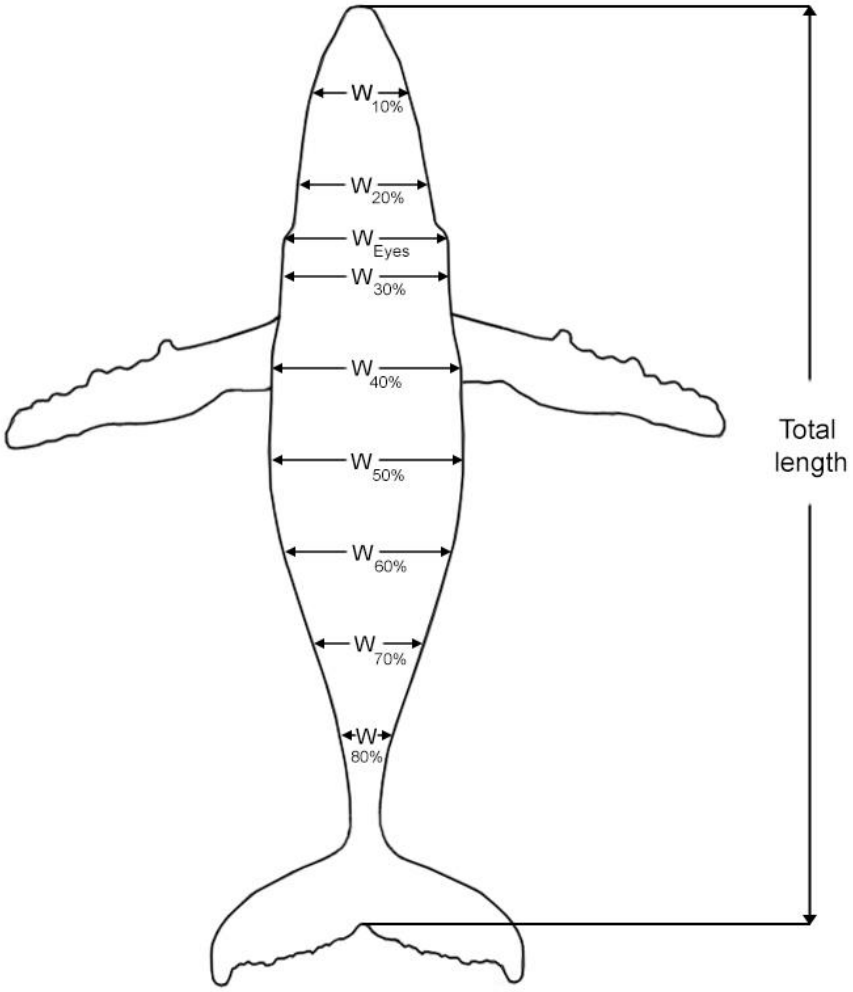

Figure 3.2. Top view of a humpback whale showing the measurement sites determined in this study for photogrammetry. Body length was measured between the tip of the rostrum and the tail notch. Body width $W_{X\%}$ was measured at sites every 10% of the whale's length from the tip of the rostrum to the location 80% of total body length, also between the eyes.

In addition, calf body length measurements were converted into proportional lengths relative to their mothers; by dividing calf body length by their mother's body length. These 'proportional' calf body lengths were used as indicators of calf growth.

3.3.5 Precision of sampling protocol

Measurements of whales can be affected by both water clarity and the position of the whale in the water (Perryman and Lynn, 2002, Miller et al., 2012). Body measurements were only determined if the whales were at the water surface, their body was lying in a flat plane (i.e. not flexed) and their body outline was clearly visible. Similar to Miller et al. (2012), if the quality of the body outline was diminished (i.e. not totally clear) on one side but still visible, the whale was measured; but if the outline quality was diminished on two sides the whale was not measured. To assess the precision of this sampling protocol, we calculated the mean coefficients of variation (CVs) of relative measurements made for lactating cows (n=10) and calves (n=5**)** that remained on the surface for long enough to be photographed in three separate passes on the same sampling flight.

3.3.6 Statistical Analyses

3.3.6.1 Identification of energy storage sites along the body

To identify the locations along the body that were the best indicators of energy storage, we investigated the difference in relative width measurements along the body between lactation stages of the mothers (early and mid-lactation) and development stages of the calves (neonate and post-neonate). These were independently assessed for cows and calves, as lactating cows are utilising energy stores while calves are accumulating energy stores. We used each of the relative width measurements along the body (between 10% - 80% of the body length in increments of 10%) as the response variables in linear models and lactation/development stage as the explanatory variables. Calves nearing independence and their late lactating mothers (n=2) were included in plots but excluded in statistical analyses, as the sample sizes were too small for modelling. We fitted linear models in *R* (R v 3.4.2) (R Development Core Team, 2017) using a Gaussian distribution with the statistical packages *nlme* (Pinheiro et al., 2013) and

MuMIn (Barton, 2014). For each location along the body, two models were fitted; a null model (with no explanatory variables) and the model that included stage as an explanatory variable. Model selection was undertaken using Akaike's Information Criterion corrected for small samples (AIC*c*) (smallest is best) and the AIC*c* weight (*w*AIC*c*) (Burnham and Anderson, 2002, Burnham et al., 2011). The AIC weight varies from 0 (no support) to 1 (complete support) relative to all models in the set (Burnham and Anderson, 2002). Where models' AICc were within 2 values, they were considered equal, and under the principal of parsimony the simplest model (one with the least terms) was selected. The proportion of variance in the response variable (R^2) was used to quantify goodness-of-fit to the data (Burnham and Anderson, 2002).

The most dominant energy storage site along the body, and thus the best index of body condition, was then identified as the one with the greatest difference in relative width between lactation/development stage, out of those models outlined above that illustrated an effect of stage.

3.3.6.2 Seasonal and annual differences in cow body condition index and calf growth

To investigate the costs of lactation we tested the seasonal and annual differences in the index of cow and calf body condition (described above) and calf length. We used linear models with a Gaussian distribution and model selection as above to examine the relationship between the body condition index, and year and stage (early / mid lactation for adult females and neonate / post-neonate development for calves) fitting all combinations of these predictor variables including the interaction. For calves we also examined the relationship between proportional length and year and developmental stage using the same process as above. Lactating females and dependent calves were analysed separately due to differences in their energy budget (i.e. females were expending energy while calves were accumulating energy).

3.3.6.3 Relationship between female body condition and calf growth

To investigate the effects of maternal body condition on calf body condition and growth, we modelled the calf body condition index and proportional calf length (relative to the mother) as a function of the female body condition index. We did this for the neonate calves and their early lactating mothers only, as mothers in mid-lactation had been transferring energy to their post-neonate calves for some time and their body condition at parturition was not known. We assumed that the mothers of neonate calves had been lactating for only a short time period and thus used their body condition as a proxy for body condition at parturition.

3.4 Results

A total of 168 humpback whales were measured over the two seasons of sampling, consisting of 82 and 86 individuals in 2013 and 2015, respectively. The 2013 samples consisted of 42 lactating cows and 40 dependent calves, including 18 cows in early lactation, 24 cows in mid lactation, 23 calves that were neonates and 17 calves that were post-neonates. The 2015 samples consisted of 46 lactating cows and 40 dependent calves; with 27 of the cows in early lactation, 17 in mid lactation and 2 in late lactation. The 40 calves consisted of 29 neonates, 9 post-neonates and 2 calves nearing independence.

Of the 88 lactating females and 80 calves, 49 were pairs where both individuals satisfied our sampling protocol in the same frame and thus both could be measured (23 and 26 pairs in 2013 and 2015 respectively).

3.4.1 Precision of sampling protocol

Mean CVs of relative width for humpback whale cows and calves at locations between 10% and 80% along the body from the rostrum to the posterior of the whale at 10% increments and between the eyes (Figure 3.2) are displayed in Table

3.1. Mean CVs were smaller for cows than for calves; and ranged between a minimum of 0.020 (width ratio at 20%) to a maximum of 0.113 (width ratio at 80%) for lactating cows, and between a minimum of 0.035 (width ratio at 30%) and maximum of 0.144 (width ratio at 80%) for dependent calves (Table 3.1). This level of sampling precision is consistent with that from other photogrammetric studies on large cetaceans (Best and Ruther, 1992, Perryman and Lynn, 2002, Miller et al., 2012). Similar to the aforementioned studies, the CVs tended to be greatest at the narrowest parts of the body, such as anterior region of the head and the posterior end of the caudal region, particularly at the narrowest location (i.e. at 80%).

Table 3.1. Mean coefficients of variation (CV) of humpback whale relative body width at each measurement site (every 10% of the body length from the tip of the rostrum to the tail notch and between the eyes) for lactating females (mothers) and dependent calves that were measured in three passes.

Age class	Sample size (No. of individuals with 3 images)	Mean CV at each measurement site on the body								
		10%	20%	Between the eyes	30%	40%	50%	60%	70%	80%
Mothers	10	0.038	0.020	0.022	0.021	0.027	0.031	0.034	0.043	0.113
Calves	5	0.071	0.044	0.066	0.035	0.053	0.057	0.075	0.072	0.144

3.4.2 Statistical Analyses

3.4.2.1 Identification of energy storage sites along the body

The relative body width of humpback whale cows in early and mid-lactation was greatest at 40% - 50% of the body length from the rostrum, and thinned progressively from the widest point towards the anterior and posterior ends of the body (Figure 3.3a). Linear models showed that relative body width measurements between early and mid-lactating cows varied at all sites along the body between 30% and 70% body length, but did not vary at sites along the head (10 - 20% body length and between the eyes) or on the peduncle (80% body length) (Table 3.2). Lactation

stage accounted for 33, 37 and 31% of the variance in relative body width at 40, 50 and 60% body length, respectively (Table 3.2) indicating that lactation stage is a strong predictor of relative body width at these sites of the body in humpback whale cows. Along with being the widest site during early and mid-lactation, the site at 50% body length also showed one of the greatest width variations (Figure 3.3a), illustrating that it is a dominant energy storage depot for lactating cows. It was thus selected as the site to be used as the index for body condition.

Figure 3.3. Mean and SD relative body widths measured at increments every 10% of the body length from the rostrum and between the eyes using aerial photogrammetry, of a) lactating cows for each stage of lactation (early, mid and late) and b) calves for each stage of development (neonate "neo", post-neonate "post" and near independence "ni"). Note that 'late' lactating cows, and calves 'near independence' displayed in this figure, were not included in the statistical analysis due to low n (n=2).

Cows in late lactation (i.e. those nursing calves nearing independence) were substantially thinner than those in early or mid-lactation. The widest part of these females, who had been lactating for an estimated 10.5 months (Chittleborough, 1958, Clapham et al., 1999), was between the eyes. From the position at the eyes, their bodies thinned progressively towards the posterior end, and also towards the anterior end (i.e. the head) (Figure 3.3a). Notably, these females were thinner in the

head region, particularly at the 20% site, than those feeding either neonate or post-neonate calves) (Figure 3.3a). This suggests that energy is stored in the head region, in the tissue surrounding the lower jaw (as the upper jaw is thinner and thus not measured), and is potentially a useful site for identifying energetically compromised individuals. As these results are based on a small sample size (n=2), they could not be tested statistically and thus need to be verified in future studies with larger sample sizes.

Table 3.2. Ranked (by smallest AIC*c*) linear models investigating the relationship between lactation stage (lac stage, early and mid) and relative width of humpback whale cows (rw) at each site along the body (10-80% of the body length from the rostrum and at the eyes). Shown are the number of parameters in the model (k), maximum log-likelihood (LogLik), Akaike's information criteria corrected for small samples (AIC*c*), change in AIC*c* relative to the top ranked model (ΔAIC*c*), AIC*c* weights (*w*AIC*c*) and the proportion of variance explained (R^2). Models in bold indicate support for the model with lactation stage over the null model (~1).

Model	*k*	LogLik	AIC*c*	ΔAIC*c*	*w*AIC*c*	R^2
rw_{10} ~ lac stage	3	310.58	-614.90	0	0.53	0.03
rw_{10} ~ 1	2	309.41	-614.70	0.20	0.48	<0.01
rw_{20} ~ 1	2	291.52	-578.90	0	0.63	<0.01
rw_{20} ~ lac stage	3	292.06	-577.80	1.06	0.37	0.01
rw_{eyes}~ 1	2	292.15	-580.20	0	0.65	<0.01
rw_{eyes} ~ lac stage	3	292.61	-578.90	1.23	0.35	0.01
rw_{30} ~ lac stage	**3**	**304.19**	**-602.10**	**0**	**0.77**	**0.05**
rw_{30} ~ 1	**2**	**301.88**	**-599.60**	**2.46**	**0.23**	**<0.01**
rw_{40} ~ lac stage	**3**	**281.44**	**-556.60**	**0**	**1.00**	**0.33**
rw_{40} ~ 1	**2**	**264.20**	**-524.30**	**32.33**	**0.00**	**<0.01**
rw_{50} ~ lac stage	**3**	**271.01**	**-535.70**	**0**	**1.00**	**0.37**
rw_{50} ~ 1	**2**	**251.43**	**-498.70**	**37.03**	**0.00**	**<0.01**
rw_{60} ~ lac stage	**3**	**253.90**	**-501.50**	**0**	**1.00**	**0.31**
rw_{60} ~ 1	**2**	**238.06**	**-472.00**	**29.55**	**0.00**	**<0.01**
rw_{70} ~ lac stage	**3**	**260.70**	**-515.10**	**0**	**0.99**	**0.12**
rw_{70} ~ 1	**2**	**255.06**	**-506.00**	**9.14**	**0.01**	**<0.01**
rw_{80} ~ 1	2	294.47	-584.80	0	0.74	<0.01
rw_{80} ~ lac stage	3	294.49	-582.70	2.12	0.26	<0.01

Humpback whale calves were widest at 30% - 50% of the body length from the rostrum with their relative body width decreasing progressively towards both the anterior and posterior ends of the body (Figure 3.3b). Linear models illustrated that

calf relative body width varied between the neonate and post-neonate development stages at the sites 20% and 70% from the rostrum (Table 3.3). These models accounted for 9 and 7% of the variation, respectively, (see R^2 values in Table 3.3) illustrating that development stage is only a weak predictor of relative body width of young calves (between the neonate and post-neonate developmental stage). The site at 70% body length showed the greatest width variations (Figure 3.3b), and was thus selected as the index site.

Table 3.3. Ranked (by AIC*c*) linear models of each of the humpback whale calf relative body width measurements (rw) at each site along the body explained by developmental status (neonate and post-neonate). Shown are the number of parameters in the model (k), maximum log-likelihood (LogLik), Akaike's information criteria corrected for small samples (AIC*c*), change in AIC*c* relative to the top ranked model (ΔAIC*c*), AIC*c* weights (*w*AIC*c*) and the proportion of variance explained (R^2). Models in bold indicate support for the model with lactation stage over the null model (~1).

Model	*k*	LogLik	AIC*c*	ΔAIC*c*	*w*AIC*c*	R^2
rw_{10} ~ 1	2	257.40	-510.60	0	0.75	<0.01
rw_{10} ~ status	3	257.41	-508.50	2.16	0.25	<0.01
rw_{20} ~ status	**3**	**228.68**	**-451.00**	**0**	**0.94**	**0.09**
rw_{20} ~ 1	**2**	**224.89**	**-445.60**	**5.41**	**0.06**	**<0.01**
rw_{eyes} ~ status	3	235.81	-465.30	0	0.60	0.03
rw_{eyes} ~ 1	2	234.33	-464.50	0.79	0.40	<0.01
rw_{30} ~ 1	2	230.58	-457.00	0	0.74	<0.01
rw_{30} ~ status	3	230.63	-454.90	2.07	0.26	<0.01
rw_{40} ~ 1	2	228.07	-452.00	0	0.72	<0.01
rw_{40} ~ status	3	228.20	-450.10	1.91	0.28	<0.01
rw_{50} ~ 1	2	217.00	-429.80	0	0.68	<0.01
rw_{50} ~ status	3	217.32	-428.30	1.52	0.32	0.01
rw_{60} ~ status	3	206.61	-406.90	0	0.69	0.05
rw_{60} ~ 1	2	204.72	-405.30	1.63	0.31	<0.01
rw_{70} ~ status	**3**	**221.59**	**-436.80**	**0**	**0.87**	**0.07**
rw_{70} ~ 1	**2**	**218.58**	**-433.00**	**3.85**	**0.13**	**<0.01**
rw_{80} ~ status	3	250.97	-495.60	0	0.62	0.04
rw_{80} ~ 1	2	249.39	-494.60	1.00	0.38	<0.01

Assuming that peak occurrence of neonate calves at NW Cape is ~7 August (Chittleborough, 1958, Irvine, unpublished data) and peak occurrence of female-calf pairs in Exmouth Gulf is ~19 September (Irvine, personal observation), the age of the

post-neonate calves is approximately 6 weeks (i.e. ~43 days). Relative body width measurements appeared to vary substantially between the post-neonate calves (~6 weeks of age) and those nearing independence (~10.5 months of age), particularly between 30% - 70% body length (Figure 3.3b), indicating that relative calf width and thus body condition increases substantially sometime after approximately 6 weeks of age. However, as the sample size of the calves nearing independence was small (n=2), these results could not be tested statistically and thus need verifying in the future with larger sample sizes.

3.4.2.2 Seasonal and annual differences in cow body condition index and calf growth

A) BODY CONDITION INDEX CHANGES IN LACTATING COWS

The highest ranked model explaining female body condition included the interaction of the predictor variables year and lactation stage (*w*AIC*c* = 0.74), and accounted for 43% of the variance in the response variable (Table 3.4). This demonstrated that the body condition index of lactating females decreased each season between early and mid-lactation and that the rate of this decrease varied between years, with female body condition declining more rapidly in 2015 than in 2013 (Figure 3.4).

Table 3.4. Ranked (by AIC*c*) linear models of humpback whale body condition index (50% body length) explained by lactation stage (early and mid) and year (2013 and 2015). Shown are the number of parameters in the model (k), maximum log-likelihood (LogLik), Akaike's information criteria corrected for small samples (AIC*c*), change in AIC*c* relative to the top ranked model (ΔAIC*c*), AIC*c* weights (*w*AIC*c*) and the proportion of variance explained (R^2).

Model	*k*	LogLik	AIC*c*	ΔAIC*c*	*w*AIC*c*	R^2
~lactation stage + year + lactation stage*year	5	275.66	-540.60	0	0.74	0.43
~lactation stage + year	4	273.20	-537.90	2.67	0.20	0.40
~lactation stage	3	271.01	-535.70	4.84	0.07	0.37
~1	2	251.43	-498.70	41.87	<0.01	<0.01
~year	3	251.59	-496.90	43.68	<0.01	<0.01

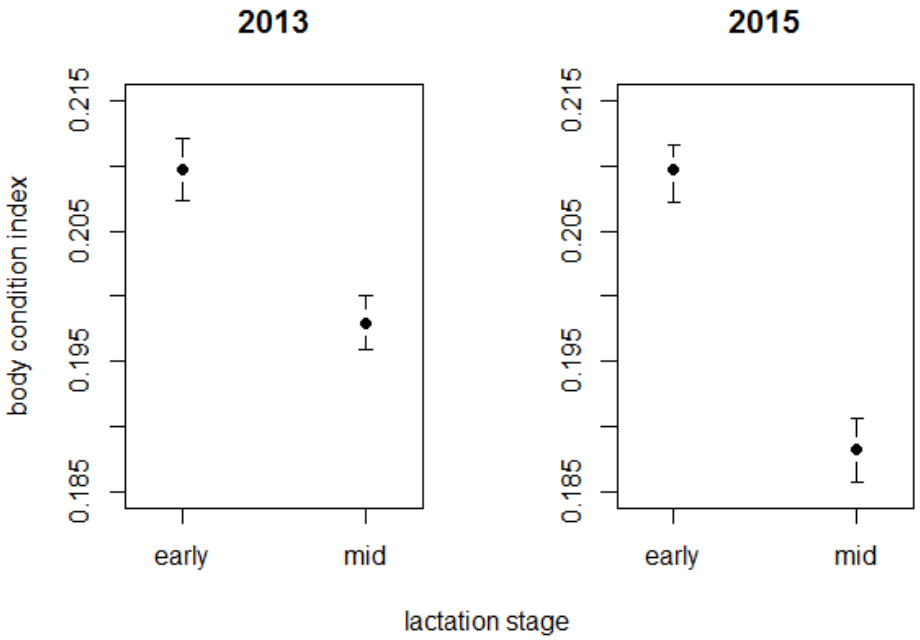

Figure 3.4. Predicted values (mean and 95% CI) from the model used to explain the relationship between body condition index (estimated by the width ratio at 50% body length) and lactation stage (early and mid) for humpback whale females in 2013 and 2015.

The relative body width at 50% body length (mean ± SD) of humpback whale females decreased from 0.21 ± 0.01 to 0.20 ± 0.01 between early and mid-lactation in 2013 and from 0.21 ± 0.01 to 0.19 ± 0.01 and 0.16 ± 0.01 between early, mid, and late lactation in 2015. Assuming a mean body length of 13.07 m for lactating females (Irvine et al., 2017b), these values correspond to approximate body widths of 2.74 ± 0.10 m and 2.59 ± 0.15 m in 2013, and 2.74 ± 0.12 m, 2.46 ± 0.15 m and 2.08 ± 0.15 m in 2015 and width reductions of 15.3 cm and 28.0 cm between early and mid-lactation in 2013 and 2015, respectively, with a further 37.9 cm reduction between mid and late lactation in 2015, for an overall width loss of 65.9 cm over the entire lactation period. Assuming the calves are weaned at ~10.5 months of age (Chittleborough, 1958), lactating females lost an estimated 0.36 cm/day (2.50 cm/week) and 0.65 cm/day (4.56 cm/week) over the 43 days (~6 weeks) between early and mid-lactation in 2013 and 2015 respectively and then a further 0.14 cm/day (0.96 cm/week) over the 276 days (39 weeks) between mid and late lactation in 2015.

B) *BODY CONDITION INDEX CHANGES IN CALVES*

The highest ranked model describing calf body condition index (estimated by the relative width at 70% body length) was the model that included the predictor variable of calf developmental stage only (*w*AIC*c* = 0.48) which accounted for 7% of the variation (Table 3.5). There was some evidence that the body condition index increase between neonates and post-neonates varied between years (*w*AIC*c* = 0.24) (Table 3.5), with a slightly greater body condition increase in 2013 than in 2015 (Figure 3.5), however developmental stage was a stronger predictor. The body condition index (mean ± SD) of humpback whale calves increased from 0.095 ± 0.012 to 0.105 ± 0.017 and 0.140 ± 0.001 between the neonate, post-neonate and near independent stages respectively (Figure 3.3b).

Table 3.5. Ranked (by AIC*c*) linear models of humpback whale calf body condition index at 70% body length explained by developmental stage (neonate and post-neonate) and year (2013 and 2015). Shown are the number of parameters in the model (k), maximum log-likelihood (LogLik), Akaike's information criteria corrected for small samples (AIC*c*), change in AIC*c* relative to the top ranked model (ΔAIC*c*), AIC*c* weights (*w*AIC*c*) and the proportion of variance explained (R^2).

Model	*k*	LogLik	AIC*c*	ΔAIC*c*	*w*AIC*c*	R^2
~stage	3	221.59	-436.80	0	0.48	0.07
~stage + year	4	221.99	-435.40	1.41	0.24	0.08
~stage + year + stage*year	5	222.76	-434.70	2.17	0.16	0.10
~1	2	218.58	-433.00	3.85	0.07	<0.01
~year	3	219.47	-432.60	4.23	0.06	0.02

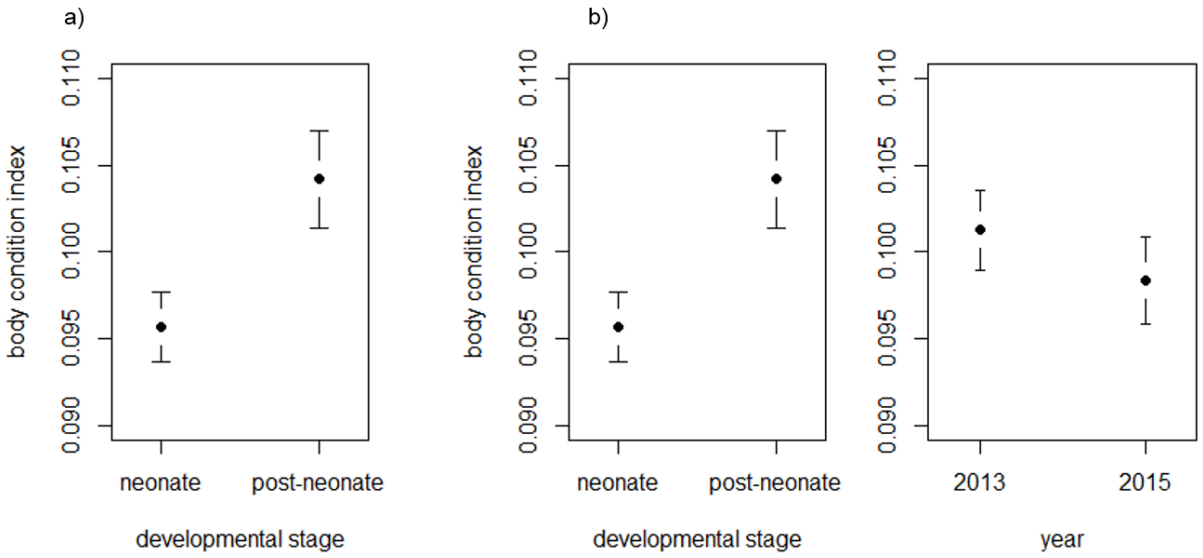

Figure 3.5. Predicted values (mean and 95% CI) from a) the top model and b) 2nd top ranked model, used to explain the relationship between calf body condition index (estimated by the relative width ratio 70% body length) and developmental stage in 2013 and 2015.

C) *CALF BODY LENGTH*

For the model investigating proportional calf length, there was equal support for the model with year and lactation stage (*w*AIC*c* = 0.42) and the model including the interaction between these two terms (*w*AIC*c* = 0.43), and accounting for around 80% of the variance in the response variable (Table 3.6). This demonstrated that the body length of calves increased each season between early and mid-lactation and that the rate of this increase varied between years, with length increasing more rapidly in 2013 than in 2015 (Figure 3.6). The year effect was small with the majority of the variation in proportional body length (78%) being explained by calf developmental stage (Table 3.6).

Table 3.6. Ranked (by AIC*c*) linear models of humpback whale calf proportional body length (relative to mother) explained by developmental stage (neonate / post-neonate) and year (2013 and 2015). Shown are the number of parameters in the model (k), maximum log-likelihood (LogLik), Akaike's information criteria corrected for small samples (AIC*c*), change in AIC*c* relative to the top ranked model (ΔAIC*c*), AIC*c* weights (*w*AIC*c*) and the proportion of variance explained (R^2).

Model	*k*	LogLik	AIC*c*	ΔAIC*c*	*w*AIC*c*	R^2
~stage + year + stage*year	5	113.47	-215.50	0	0.43	0.81
~stage + year	4	112.19	-215.40	0.04	0.42	0.80
~stage	3	109.92	-213.30	2.19	0.15	0.78
~year	3	75.36	-144.20	71.30	<0.01	0.05
~1	2	74.04	-143.80	71.66	<0.01	<0.01

Proportional calf length (mean ± SD) increased from 0.38 ± 0.02 to 0.48 ± 0.03, of the mothers body length, between the neonate and post-neonate stages in 2013 and from 0.37 ± 0.02 to 0.45 ± 0.03 and 0.63 ± 0.03 between the neonate, post-neonate and near independent stages in 2015 (Figure 3.7). At a mean length of 13.07 m for lactating females (Irvine et al., 2017b), these values correspond to 4.97 ± 0.33 and 6.31 ± 0.36 m for neonates and post-neonates in 2013, respectively, and 4.88 ± 0.23, 5.93 ± 0.29 and 8.19 ± 0.33 m for neonates, post-neonates and calves nearing independence in 2015. This corresponds to a body length increase of 1.34 m (3.1 cm/day; 21.8 cm/week) between the neonate and post-neonate stages (~43 days) in 2013 and 1.05 m (2.4 cm/day; 17.1 cm/week) and a further 2.25 m length increase between post-neonate stage and near independence (0.82 cm/day; 5.72 cm/week) in 2015. The total body length increase during the 10.5 months of suckling is approximately 3.31 m - a length increase of approximately 68%.

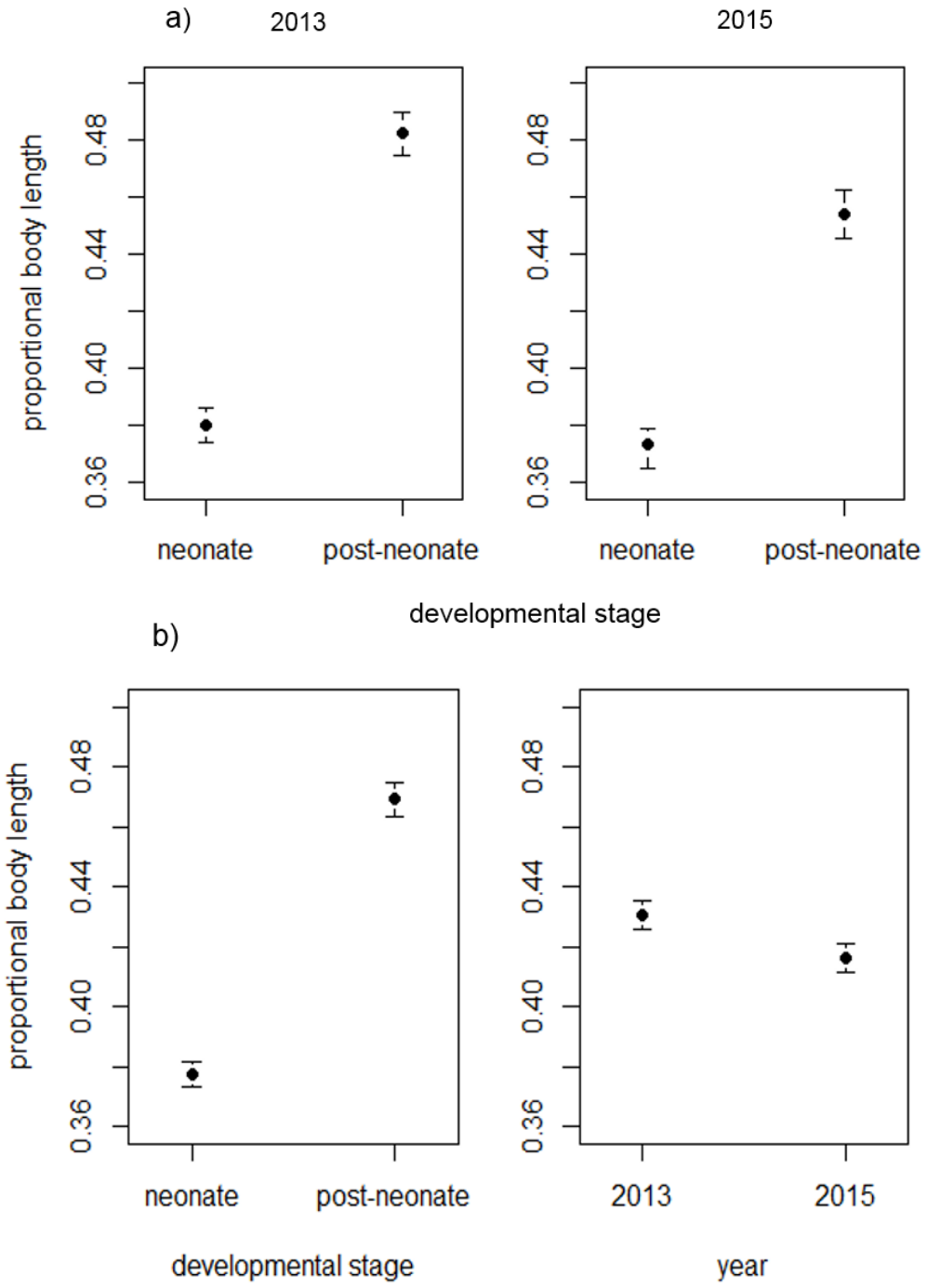

Figure 3.6. Predicted values (mean and 95% CI) from the two top ranked models used to explain proportional body length of humpback whale calves: a) the model showing the relationship between proportional body length and the interaction between the predictor variables calf developmental stage and year for humpback whale calves in 2013 and 2015; and b) the model showing the relationship between proportional body length and the predictor variables calf developmental stage and year.

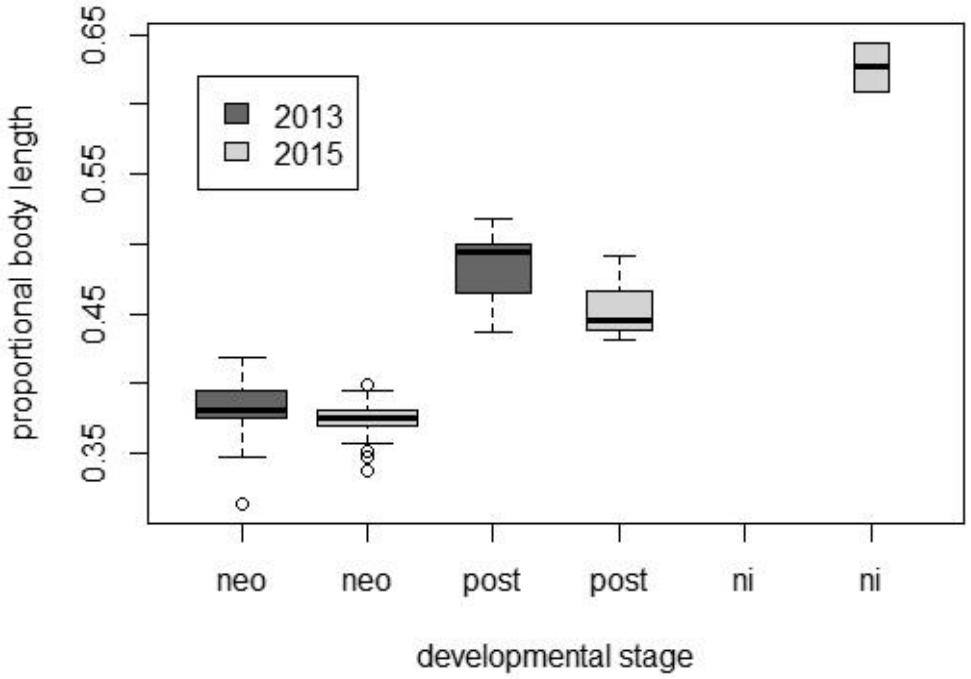

Figure 3.7. Boxplots showing the proportional body length (relative to the mother) of humpback whale calves at different developmental stages (neonate "neo", post-neonate "post" and near independence "ni") in 2013 and 2015. The boundaries of each box represent the interquartile range (25% - 75%); the solid line inside the box is the median. The whiskers represent the 9 – 91% range; suspected outliers are represented by open circles.

3.4.2.3 Relationship between female body condition and calf growth

Linear models illustrated that there was no relationship between the body condition index of the early lactating females and either the body condition index (null model: *w*AIC*c* = 0.75), or the proportional length of their neonate calves (null model: *w*AIC*c* = 0.77).

3.5 Discussion

In this study we have successfully demonstrated the viability of using photogrammetric techniques as an index of body condition, to quantify relative differences in the intra- and inter-annual body condition in free swimming humpback whale cows and their accompanying calves. We identified dominant energy storage

sites along the body and suggest that their quantification provides an index for monitoring the energy stores of free-swimming humpback whales during their annual migration. As expected we found a decrease in female energy stores (body condition) and a rapid increase in calf length between early and mid-lactation, highlighting the importance of maternal energy stores for offspring development (Wheatley et al., 2006). Importantly, we found that the rate of body condition decline in the lactating females was greater in 2015 than in 2013, but that the additional energy expenditure was not transferred into calf growth. This indicates that either maternal energy stores were diverted to activities other than lactation in 2015 (McMahon and Burton, 2005, Wheatley et al., 2006, McMahon et al., 2017), or that energy stores in 2013 were higher than in 2015 but stored differentially in reserves that were not visible in body width measurements e.g. in the bone (Tomilin, 1957, Slijper, 1962). Both scenarios result in slower calf growth and highlight the importance of maximising maternal energy stores and the allocation to offspring development. Our analyses provide valuable information about temporal variations in maternal energy stores, and their allocation, that can be used as a baseline to assess individual or population health. Extended over long time frames, such data can be used as a condition index to assess trends in population health or to monitor environmental change and ecosystem health.

We found that the site midway along the body (at 50% body length) was the widest and most variable location of lactating cows between early and mid-lactation, suggesting that it is an important energy storage site for humpback whales. This has also been found for gray and right whales (Perryman and Lynn, 2002, Miller et al., 2012), while for balaenopterids such as fin (*Balaenoptera physalus*), sei (*Balaenoptera borealis*) and minke (*Balaenoptera acutorostrata*) whales, the caudal region behind the dorsal fin appears to be an important energy storage area (Lockyer et al., 1985, Lockyer, 1987, Næss et al., 1998). It thus appears that cetacean energy stores are distributed heterogeneously within the body in a manner that differs

between the slow swimming species with robust body shape (Ford and Reeves, 2008) and high proportions of blubber (Rice and Wolman, 1971, Lockyer, 1981b), and the fast swimming species with streamlined bodies and high proportions of muscle (Lockyer, 1981b).

Although, we found that the body condition index at 50% body length was the most variable for the lactating cows, the body condition index at 70% body length was the most variable for the young calves. This may be due to development of musculature in the caudal region during the rapid travel period that follows parturition (Thomas and Taber, 1984, Cartwright and Sullivan, 2009b). The body condition index at this site may thus be more indicative of changes in body proportions that occur during early calf development (Lockyer, 1981b), rather than the accumulation of energy stores. Our results thus suggest that, during early calf development, maternal energy stores are allocated to the rapid post-partum somatic growth that is typical in baleen whale calves (Lockyer, 1981b, Best and Ruther, 1992, Perryman and Lynn, 2002, Fortune et al., 2012, Christiansen et al., 2018), rather than increases in body condition. It is noteworthy that the widest and most variable site between post-neonate calves and those nearing independence was at 50% body length (i.e. the same as that of the lactating cows), suggesting that the site most appropriate for estimating body condition of young calves may need further evaluation. However, larger sample sizes of calves nearing independence are required to investigate this further.

The body condition decline we found for lactating cows in the breeding grounds is consistent with that measured for other baleen whales including southern right whales (Miller et al., 2012) and gray whales (Perryman and Lynn, 2002). This illustrates the high costs of simultaneous lactation and fasting that is typical of baleen whales in the oligotrophic breeding grounds (Chittleborough, 1965, Lockyer, 1981b). Energy stores are critical for mammalian survival, particularly in times of nutritional stress, such as fasting or lactation (Young, 1976). The typically poor body

condition of lactating baleen whales (Lockyer, 1981b, Perryman and Lynn, 2002, Miller et al., 2012) highlights the importance of large energy stores for capital breeders (e.g. Irvine et al., 2017b) who fuel reproduction with stored energy reserves (Stearns, 1992, Jönsson, 1997). Large energy stores would be particularly important for females that calve annually (Chittleborough, 1958) and are thus simultaneously lactating and gestating throughout long periods of fasting.

The body condition decline was more rapid between early and mid-lactation when lactation was fuelled exclusively by energy stores in the breeding grounds, than between mid and late lactation when a period of food intake in the Antarctic feeding grounds (approximately 4.5 months) presumably supplements lactation (Dawbin, 1966). However, the relatively thinner bodies of the late lactating females (after departure from the Antarctic feeding grounds) compared to the mid-lactating females indicates that the food intake in the Antarctic feeding grounds was not sufficient to satisfy the high energetic costs typical of mammals during late lactation (Millar, 1977), forcing them to continue drawing off stored energy reserves. Breeding females thus appear to experience a net energy loss for the entire 10.5 months of lactation, which will continue after calf weaning when they will be back in the breeding grounds (Chittleborough, 1965, Dawbin, 1966). Given the energy depleted state of their bodies (i.e. very thin), these late lactating cows may be prone to exhausting their finite store of energy reserves before they return to their feeding grounds (e.g. Le Boeuf et al., 2000). It is important to note however, that these late lactating cows (sampled in mid-August) may have lactated for longer than the average 10.5 months, given that weaning typically occurs in June (Chittleborough, 1958). Consequently, they may be thinner than the majority of females during late lactation.

The mean growth rate of the calves during early development (~2.8cm/day) is consistent with that found for other baleen whale calves (i.e. 2.8 cm/day for both southern right (Best and Ruther, 1992) and gray whale calves (Perryman and Lynn,

2002); 2.4 cm/day for fin whale calves, 3.45 cm/day for blue whale calves (Lockyer, 1981b) and (3.3 cm/day) for post-neonate humpback whale calves (Christiansen et al., 2016)). Baleen whales have one of the most rapid offspring growth rates of all mammals (Frazer and Huggett, 1974), with weights of calves increasing more than tenfold in their first year of life (Lockyer, 1981b) and lengths reaching 63% to 75% of adult body length by the time of independence (Clapham et al., 1999, Fortune et al., 2012). Terrestrial mammals, in comparison, reach an average of 37% of adult body size at independence (Millar, 1977). As weaning size in mammals is known to influence individual survival (McMahon et al., 2000, McMahon et al., 2015), rapid growth rate is important for maximising offspring survival rates. This highlights the importance of stored energy reserves in enabling rapid and efficient energy transfer to offspring (Oftedal, 1997). Rapid growth during dependency may improve calf survival through a variety of processes including increasing swimming and diving capabilities (Thomas and Taber, 1984, Irvine et al., 2000), defending against predation (Pitman et al., 2014) and increasing insulation for the cold Antarctic waters (Corkeron and Connor, 1999). For long distance migrants, such as many baleen whales, rapid somatic growth during early development may be essential for successful migration.

In contrast to length, calf body condition increased only slightly during the early stages of development in the breeding grounds (i.e. between the neonate and post-neonate stages) and then more substantially during the latter stages of development, as they neared independence. Although information on body condition of baleen whales calves is scant, other studies also show little or no increase in body condition during early development (Miller et al., 2012, Christiansen et al., 2016) and consistently good body condition at weaning (Bradford et al., 2012). This pattern of rapid somatic growth in early development followed by body condition increase during late development may represent different survival needs as the calves develop. For example, in the tropical breeding grounds, the small

neonate calves may allocate energy into increasing body size to improve swimming abilities (Taber and Thomas, 1982) and fend off predators (Pitman et al., 2014), as stated above. In the cold waters of the feeding grounds, the larger calves may increase lipid stores for insulation (Young, 1976, Rutishauser et al., 2004) and to prepare for the post-weaning fast when they will return to the oligotrophic breeding grounds (Chittleborough, 1965, Dawbin, 1966).

Cow body condition declined more rapidly in 2015 than in 2013 indicating that energy expenditure in the breeding grounds might have differed each year. That offspring growth was also slowest in 2015 suggests that energy reserves in this year were preferentially allocated to maintenance, rather than reproductive activities. This trade-off between competing fitness based traits such as survival and reproduction is central to life history theory (Stearns, 1992), particularly as both are fuelled by finite energy stores whilst in the breeding grounds. In times of resource limitation capital breeders can preferentially allocate energy to survival rather than reproduction by either transferring less energy to offspring if already invested in reproduction (McMahon and Burton, 2005, Wheatley et al., 2006, McMahon et al., 2017), or by skipping or delaying breeding (Desprez et al., 2017). This strategy provides a buffering mechanism which maximises adult survival in times of environmental fluctuations (Forcada et al., 2008), however it can reduce offspring survival and reproductive success (McMahon et al., 2000) and thus effect population dynamics (Clausius et al., 2017b). Unfortunately, we were not able to distinguish body condition loss from maintenance activities and reproductive activities, as non-pregnant females were not sampled. However, future studies could include different reproductive classes in order to explore these differences in energy expenditure.

Maintenance costs in the breeding grounds could differ from a variety of causes that affect metabolism or activity levels such as differing water temperatures (Brodie, 1975), rough water conditions (Norris, 1967), anthropogenic disturbance (Christiansen et al., 2014a), harassment by conspecifics (Cartwright and Sullivan,

2009a), or differences in travel costs by travelling to different destinations (e.g. Double et al., 2012, Riekkola et al., 2018). Cetacean travel costs are thought to be higher for mothers with calves, than for other components of the population, possibly due to the requirement of surfacing more frequently and swimming in echelon formation (Williams and Noren, 2009).

Differences in energy expenditure in the breeding grounds can be substantial. For example lactating mothers in the Hawaiian breeding grounds expended 30% more energy when harassed by males seeking breeding opportunities (Cartwright and Sullivan, 2009a). Although the reasons for different energy expenditure in this study are unclear, the varying calf growth rates highlight the effects of differing levels of maternal investment on offspring development that are typical among mammals living in a variable environment (Wheatley et al., 2006, McMahon et al., 2017). This highlights the importance of minimising energy expenditure in the breeding grounds in order to maximise the maternal energy reserves available for allocation to calf growth and development (Corkeron and Connor, 1999). Other capital breeders such as elephant seals (*Mirounga angustirostris*) minimise energy expenditure in the breeding grounds by sleeping for long periods of time and staying near the parturition site for their entire lactation period (Gittleman and Thompson, 1988). Conserving energy stores is also beneficial for the mothers who need to retain sufficient reserves for their own maintenance functions.

An alternative explanation for the varying rate of cow body condition decline may be differing energy stores at the start of lactation. Although the body condition index of early lactating females was similar in each year, energy stores may have been located in tissues not detectable in body shape measurements. In cetaceans, energy is stored as lipid in various depots throughout the body, initially in the blubber, and then in the bone, muscle, and viscera (Slijper, 1962, Lockyer, 1981b). It has been suggested that blubber may have a lipid storage threshold, due it's multi-functional role that includes buoyancy and thermoregulation in addition to energy storage

(Lockyer, 1991). As substantial amounts of lipid can be stored in the bone (i.e. nearly as much as in the blubber) (Tomilin, 1957), it is possible that more lipid was stored in the bone in 2013 and could not be detected by body width measurement. This may indicate a shortfall in methods that use morphometrics as an index of energy stores, however this can be accounted for by quantifying the change in body condition over time, such as in this study, rather than quantifying a single value at a fixed point in time.

Interestingly, the body condition of mothers was not linked to the condition or size of their neonate calves, suggesting that pre-partum investment in humpback whales does not vary with energy stores. In mammals there is a well-established link between maternal body condition and reproductive success (Young, 1976), due in part to the effects of maternal size on offspring size (Pomeroy et al., 1999) and in turn offspring survival (McMahon et al., 2000, McMahon and Burton, 2005). However, the mechanisms driving this relationship appear to be variable in marine mammals, with maternal body size being linked to a variety of offspring traits including foetal growth (Christiansen et al., 2014b), offspring birth mass (McDonald et al., 2012), offspring weaning mass (Arnbom et al., 1993) and offspring growth rates (Wheatley et al., 2006, Christiansen et al., 2018). Humpback whales may be similar to Weddell seals (*Leptonychotes weddellii*) where maternal mass influences post-partum investment, rather than pre-partum investment and is thus linked to offspring growth, rather than offspring birth mass (Wheatley et al., 2006).

That a link between mother and calf body condition has been identified in the same humpback whale population (Christiansen et al., 2016) is likely due to differences in sample design. In this study, we sampled neonate calves and their mothers during the northern migration (Irvine et al., 2017a) and used the body condition of the neonate mothers as a measure of maternal energy stores. Although we have defined neonate calves as being <1 month of age according to Kaufman and Forestell (2006), our size category of <0.42 of mother body length, places them in the size range of

newborn calves (0.3 – 0.44 mother body length) reported by Clapham (1999). Thus, although the exact age of the neonate calves is unknown, they are likely very young and thus have mothers that have been lactating for short time periods. Christiansen et al. (2016) sampled larger post-neonate calves and their mothers during their southern migration (Jenner et al., 2001) and used the body condition of the post-neonate mothers as a measure of maternal energy stores. However, as demonstrated in this study, post-neonate mothers have transferred substantial energy stores to their offspring by the post-neonate developmental stage, with cow body condition declining by ~5 - 10% and calf body condition increasing by ~10%. It is thus difficult to interpret the results of the Christiansen et al. (2016) study. We recommend that future studies investigating links between mother and calf body condition target either known-age calves, or classify calves into age groups, so that maternal energy stores can be quantified accurately and pre-partum and post-partum investment can be disentangled.

In this study, we used non-invasive photogrammetric techniques to identify important energy storage sites that can be used as an index of body condition for lactating females and their calves. In doing this, we have developed a reliable method of determining relative body condition, and have also begun to establish a baseline of humpback whale body condition that can be used to monitor population health over time. This is important as whale populations recover from over-exploitation during the last century and may start to experience density dependent changes (Williams et al., 2013) or changes due to environmental variation (Hewitt et al., 2003, Murphy et al., 2007, Nicol et al., 2008). This body condition index can also be used to compare the health status of different humpback whale populations, or other baleen whale species, around the globe and potentially provide insights into the varying rates of recovery of different populations (e.g. Bradford et al., 2012, Fortune et al., 2013).

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Chapter 4

Evidence for a widely expanded humpback whale calving range along the Western Australian coast

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4.1 Abstract

The recognised calving grounds of humpback whales (*Megaptera novaeangliae*) that breed along the Western Australian coast (Breeding Stock D) extend along the Kimberley coast between Camden Sound and Broome (15°S -18°S). However, there are reports of neonates further south, suggesting that the calving areas may be poorly defined. During aerial photogrammetric research in 2013 and 2015, we sighted large numbers of humpback whale calves along North West Cape (21°47'S - 22°43'S). We estimated the minimum relative calf abundance to be 463 - 603 in 2013 and 557 - 725 in 2015. We categorised the calves as either neonate or post-neonate according to their colour and size. The majority of calves sighted in both years (85% in 2013; 94% in 2015) were neonates. Our observations indicate that a minimum of approximately 20% (17.1% - 24.3%) of the expected number of calves of this population are born near, or south of, North West Cape. We thus demonstrate that the calving grounds for the Breeding Stock D population extend south from Camden Sound in the Kimberley (15°S) to at least North West Cape (22°43'S), 1,000 km south west of the currently recognised calving area.

4.2 Introduction

Calving areas are a critical component in the life history of many species (Harwood, 2001) as they provide a safe haven for the young in their early and most vulnerable stages of development (Gabriele et al., 2001). Conditions experienced during early development have been shown to affect reproductive performance and survival in both mammals and birds (Lindström, 1999). Many migratory species, including baleen whales (Lockyer, 1981b) and sea birds (Berthold, 2001) travel vast distances from productive feeding grounds to areas that have appropriate conditions for rearing their young. Young marine mammals have limited diving and swimming abilities (Thomas and Taber, 1984, Mann and Smuts, 1999, Irvine et al., 2000, Rodríguez et al., 2008, Cartwright

and Sullivan, 2009b), are prone to predation (Corkeron and Connor, 1999, Ford and Reeves, 2008, Pitman et al., 2014), and are totally dependent on their mothers for nutrition (Chittleborough, 1958). Calving areas provide suitable habitat for both the young and their lactating mothers, which in some cases are using finite energy reserves for prolonged time periods (Dawbin, 1966, Lockyer, 1981b). Identifying and protecting such calving areas is important for ensuring the health of both mothers and their dependent offspring (Cartwright and Sullivan, 2009b) and thus safeguarding future generations.

Humpback whale breeding grounds are distributed in tropical coastal waters (21.2°C – 28.3°C) within 30° of the equator (Rasmussen et al., 2007). Calving, and mating take place in these areas, however, the location and extent of the calving areas are not well understood for any population. Calving areas are typically located in shallow waters, close to the coast (Ersts and Rosenbaum, 2003, Félix and Botero-Acosta, 2011, Rasmussen et al., 2012, Craig et al., 2014), which potentially exposes humpback whales to anthropogenic disturbance during a vulnerable stage in their life history.

The largest population of humpback whales worldwide, the Breeding Stock D (BSD) population (estimated at ~ 20,000 - 30,000) (Salgado Kent et al., 2012, IWC, 2014), feeds in Antarctic Management Area IV (70°E – 130°E) and migrates along the west coast of Australia (IWC, 2011). The temporal and geographical extent of its migration along the coast has been described, with a calving area identified at the northern extent, between Camden Sound and Broome (15°S - 18°S) (Jenner et al., 2001). However, during the commercial whaling period, a considerable number of neonate calves were recorded off Point Cloates (22°43'S), at the southern end of North West Cape (Chittleborough, 1953), with some being recorded as far south as Albany (35°S) (Chittleborough, 1965). More recently, substantial numbers of neonate calves have been sighted along North West Cape during aerial surveys (2008 – 2010) (authors' personal observation), boat surveys (Double et al., 2012, Pitman et al., 2014), and eco-

tourism activities.[3] Such observations suggest that the calving areas may extend further along the coast than previously thought.

During a study along North West Cape, designed for photogrammetric analysis, we recorded large numbers of neonate humpback whale calves. As this region is not recognised as a calving area (Department of the Environment and Heritage, 2005), we employed our data to determine the importance of North West Cape as a calving area by defining calf distribution and estimating minimum relative abundance in the area. These data also provide important information about the calving range and habitat use of the BSD humpback whales in a coastal area that experiences high levels of human activity.

4.3 Materials and methods

4.3.1 Aerial searches

We conducted aerial searches along North West Cape, Western Australia (figure 4.1), during July and August 2013 and 2015, to obtain vertical aerial photographs of all groups containing calves (calf groups) for photogrammetric analysis. In this study, a whale was classified as a calf if it was within close proximity to another whale and estimated to be <2/3 of the length of the accompanying animal (Clapham et al., 1999). All searches were conducted at approximately 95 knots (170 km/h) from a high-wing, light aircraft (Cessna 172), fitted with flat windows. Searches in 2013 were conducted opportunistically from spotter planes that were chartered to locate whale sharks (*Rhincodon typus*) for the ecotourism industry. These searches were flown at an altitude of 305 m (1,000 ft), in an irregular grid pattern that extended from the seaward edge of the fringing reef, out to approximately 5.5 km from the reef edge (Fig. 4.2a). Flight duration and latitudinal coverage along the coast were variable, depending on the occurrence of whale sharks on any given day (table 4.1). In

[3]Personal communication from Eric Roulston, Chief Pilot, Norwest Air Work, PO Box 909 Exmouth, 6707 Western Australia, Australia, August 2013.

general, if whale shark sightings were scarce, the latitudinal extent of the searches was increased, along with the number of times the grid patterns were repeated over the search area.

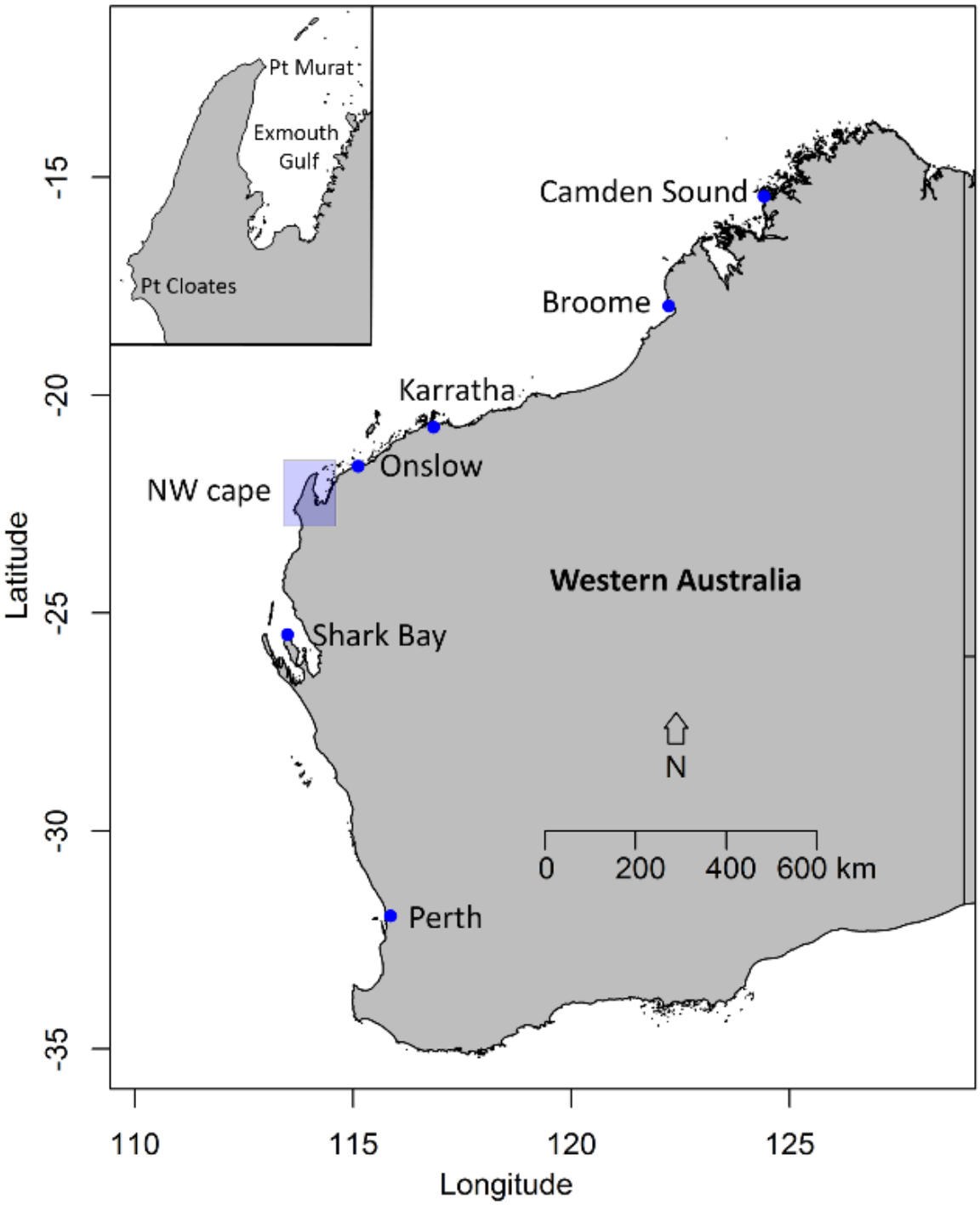

Figure 4.1. Map of Western Australia. Inset in upper left shows the location of the study area, North West Cape.

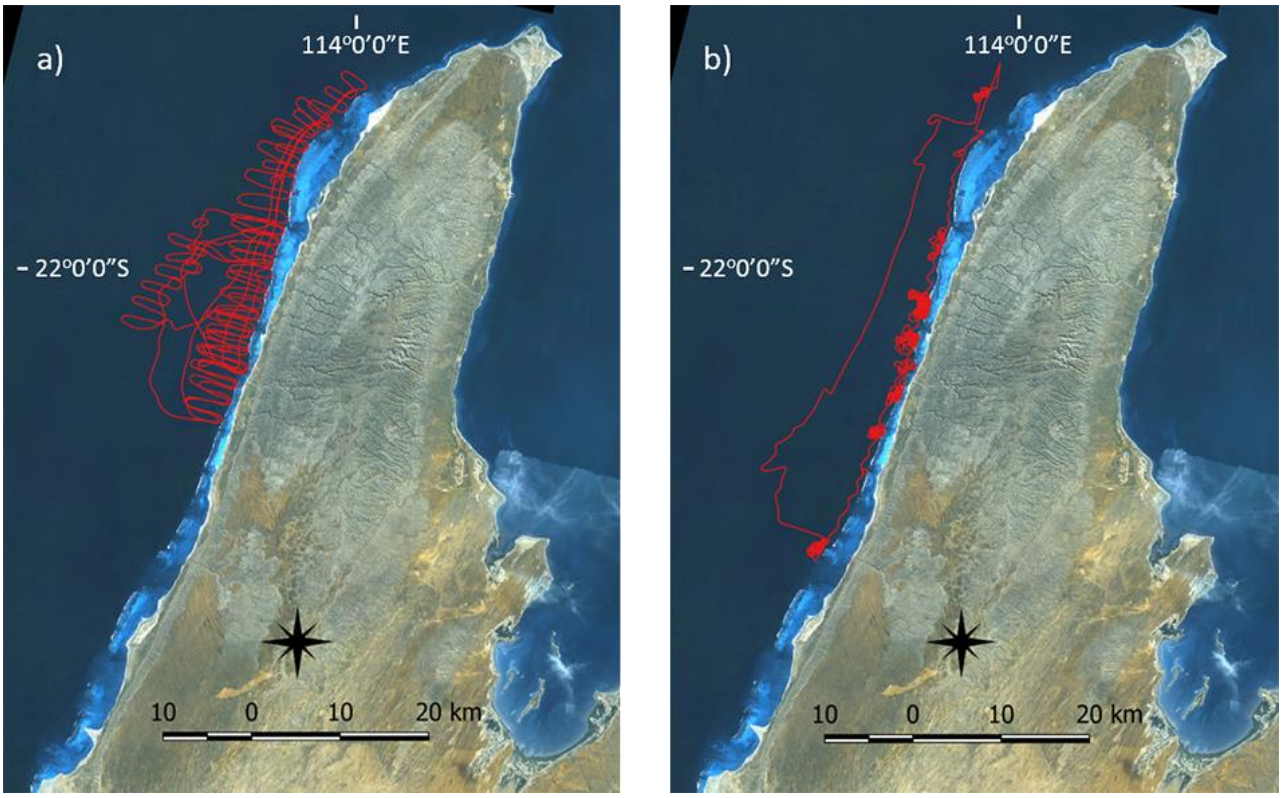

Figure 4.2. Typical search patterns of flights used to search for humpback whale calf groups along North West Cape in a) 2013: flights chartered by the whale shark industry and b) 2015: flights chartered for humpback whale research.

The 2015 flights were flown at an altitude of 245 m (800 ft) and conducted specifically to search for, and photograph, humpback whale calf groups. Search coverage was a haphazard design, targeting the area along the seaward edge of the fringing reef, where calf groups were sighted in 2013. Flights consisted of two track lines running roughly parallel to the coast: the first track was flown southwards along the reef edge - against the flow of the northward migration. Weather permitting, the return (second) track was flown northwards approximately along the 200 m depth contour (~5 - 10 km seaward of the reef edge) (figure 4.2b). This track was chosen to search the offshore waters at a sufficient distance from the first track to prevent double-counting of whale groups. All flights took place in calm weather conditions (Beaufort Sea State of ≤2) and were terminated when conditions exceeded this level. Flight duration was variable, depending on weather conditions and availability of aircraft, but averaged 1.8 h (0.7 - 3.2 h) (table 4.2).

Table 4.1. Humpback whale calves sighted along North West Cape, Western Australia, during 10 aerial surveys in 2013. Length of coast refers to the latitudinal extent of the aerial searches. Calves were categorised as 'neonates' or 'post-neonates' according to their colour and relative size i.e., neonates were light grey and approximately 1/3 the length of their mother while post-neonates were the same colour as their mother and larger than 1/3 the length of their mother. Those migrating northwards are recorded in parentheses; - no calves were sighted travelling south during the aerial searches. Confidence interval of the abundance estimate is reported in parentheses.

Flight	Date (2013)	Length of coast (km)	Search time (h)	No. calves (migrating)	No. neonates (migrating)	No. post-neonates (migrating)	Estimated daily minimum relative calf abundance (95% CI)	
							7.4 km h^{-1} Chittleborough (1953)	5.65 km h^{-1} (Salgado Kent *et al.* 2012)
1	23 July	23.4	3.2	1 (0)	1 (0)	0	0	0
2	29 July	31.3	4.1	10 (10)	9 (9)	1 (1)	56.4 (CI = 50.2 - 62.6)	43.3 (CI = 38.3 - 48.4)
3	30 July	30.8	3.7	2 (2)	2 (2)	0	11.5 (CI = 10.2 - 12.7)	8.8 (CI = 7.8 - 9.8)
4	07 August	47.3	1.9	10 (7)	7 (7)	3 (0)	26.1 (CI = 23.2 - 29.0)	20.1 (CI = 17.7 - 22.4)
5	08 August	16.5	0.8	6 (5)	5 (5)	1 (0)	53.4 (CI = 47.5 - 59.3)	41.0 (CI = 36.2 - 45.8)
6	09 August	36.1	3.9	2 (2)	2 (2)	0	9.8 (CI = 8.7 - 10.9)	7.5 (CI = 6.6 - 8.4)
7	13 August	41.7	2.0	4 (4)	4 (4)	0	16.9 (CI = 15.1 - 18.8)	13.0 (CI = 11.5 - 14.5)
8	14 August	47.4	2.8	1 (1)	1 (1)	0	3.7 (CI = 3.3 - 4.1)	2.9 (CI = 2.5 - 3.2)
9	21 August	20.6	2.4	3 (3)	3 (3)	0	25.8 (CI = 22.9 - 28.6)	19.8 (CI = 17.5 - 22.1)
10	25 August	43.0	4.7	2 (1)	1 (1)	1 (0)	4.1 (CI = 3.6 - 4.6)	3.2 (CI = 2.8 - 3.5)
Total		338.1	29.4	41 (35)	35 (34)	6 (1)	207.6 (CI = 184.7 - 230.6)	159.5 (CI = 140.9 - 178.1)
Mean		33.8	2.9	4.1 (3.5)	3.5 (3.4)	0.6 (0.1)	18.3 (CI = 16.2 - 20.3)	14.0 (CI = 12.4 - 15.7)

Table 4.2. Humpback whale calves sighted along North West Cape, Western Australia, during 11 aerial surveys in 2015. Length of coast refers to the latitudinal extent of the aerial searches. Calves were categorised as 'neonates' or 'post-neonates' according to their colour and relative size i.e., neonates were light grey and approximately 1/3 the length of their mother while post-neonates were the same colour as their mother and larger than 1/3 the length of their mother. Those migrating northwards are recorded in parentheses; - no calves were sighted travelling south during the aerial searches. Confidence interval of the abundance estimate is reported in parentheses.

Flight	Date (2015)	Length of coast (km)	Search time (h)	No. calves (migrating)	No. neonates (migrating)	No. post-neonates (migrating)	Estimated daily minimum relative calf abundance (95% CI)	
							7.4 km h^{-1} Chittleborough (1953)	5.65 km h^{-1} (Salgado Kent *et al.* 2012)
1	03 July	48.2	0.8	1 (1)	1 (1)	0	3.7 (CI = 3.3 - 4.1)	2.8 (CI = 2.5 - 3.1)
2	07 July	28.5	0.7	1 (1)	1 (1)	0	6.2 (CI = 5.5 - 6.9)	4.8 (CI = 4.2 - 5.3)
3	22 July	35.2	0.9	2 (2)	2 (2)	0	10.0 (CI = 8.9 - 11.1)	7.7 (CI = 6.8 - 8.6)
4	04 August	10.0	1.2	7 (7)	7 (7)	0	123.3 (CI = 109.7 - 137.0)	94.7 (CI = 83.7 - 105.8)
5	07 August	34.5	2.0	14 (14)	14 (14)	0	71.5 (CI = 63.6 - 79.5)	55.0 (CI = 48.5 - 61.4)
6	12 August	21.1	0.7	1 (1)	1 (1)	0	8.4 (CI = 7.4 - 9.3)	6.4 (CI = 5.7 - 7.2)
7	14 August	79.6	3.2	15 (12)	14 (12)	1 (0)	26.6 (CI = 23.7 - 29.6)	20.4 (CI = 18.1- 22.8)
8	15 August	52.3	2.1	7 (7)	6 (6)	1 (1)	23.6 (CI = 21.0 - 26.3)	18.2 (CI = 16.0 - 20.3)
9	16 August	107.4	3.0	13 (12)	12 (11)	1 (1)	19.7 (CI = 17.5 - 21.9)	15.1 (CI = 13.4 - 16.9)
10	17 August	52.2	2.2	5 (4)	4 (4)	1 (0)	13.5 (CI = 12.0 - 15.0)	10.4 (CI = 9.2 - 11.6)
11	19 August	30.2	0.7	3 (3)	3 (3)	0	17.5 (CI = 15.6 - 19.5)	13.5 (CI = 11.9 - 15.0)
Total		499.2	17.3	69 (64)	65 (62)	4 (2)	324.2 (CI = 288.3 - 360.1)	249.0 (CI = 219.9 - 278.1)
Mean		45.4	1.6	6.3 (5.8)	5.9 (5.6)	0.4 (0.2)	22.6 (20.1 - 25.1)	17.4 (15.4 - 19.4)
Total*		422.5	15.8	67 (62)	63 (60)	4 (2)	314.3 (CI = 279.5 - 349.1)	241.5 (213.2 - 269.7)
Mean*		46.9	1.8	7.4 (6.9)	7.0 (6.7)	0.4 (0.2)	25.9 (23.0 - 28.8)	19.9 (17.6 - 22.2)

* Data truncated to calves sighted between 22 July and 19 August.

4.3.2 Data collection

Survey personnel consisted of a pilot, situated on the port side of the aircraft, and an observer situated on the starboard side, both linked via an intercom system. When a calf group was sighted, the flight track was altered and the aircraft directed towards the group. During each approach, the starboard observer lent out the window, determined the direction of travel of the group and then captured a vertical photograph as the aircraft passed directly overhead. Groups travelling north were followed by one 'blank' photograph; those milling by two blank photographs; and those travelling south by three 'blank' photographs. This methodology enabled multiple observations to be recorded simply and quickly, with the use of just a digital camera.

Humpback whales were photographed using a Canon digital SLR (EOS 50D fitted with a Canon 100 mm lens in 2013, and an EOS 5D fitted with a Canon 85mm lens in 2015). The majority of calf groups (~90%) sighted in 2013 were photographed, but it was not possible to photograph all groups, as the primary purpose of the flights was whale shark spotting. In 2015, every calf group sighted was photographed. Camera time was synchronised with a handheld GPS (Garmin *GPSmap 96*) prior to each flight. The position of each calf group was identified post survey by linking the time of each photo to GPS location, using the open source software 'Geotag' (http://geotag.sourceforge.net). Bathymetry data were sourced from the Ausbath_09_V4 data set available from Esri and the water depth of each sighting was extracted in R 3.0.2 (R Development Core Team, 2013). Photographs were examined post search to extract information on group size, group composition (mother-calf or mother-calf with escort), and to classify calves. Neonates were identified by their light grey colour (Chittleborough, 1953, Kaufman and Forestell, 2006) and small relative size (~1/3 of mother body length) (Clapham et al., 1999) (figure 4.3a). Post-neonates were identified by their dark colour (similar to that of their mother)

(Kaufman and Forestell, 2006) and body length (>1/3 of mother body length) (figure 4.3b).

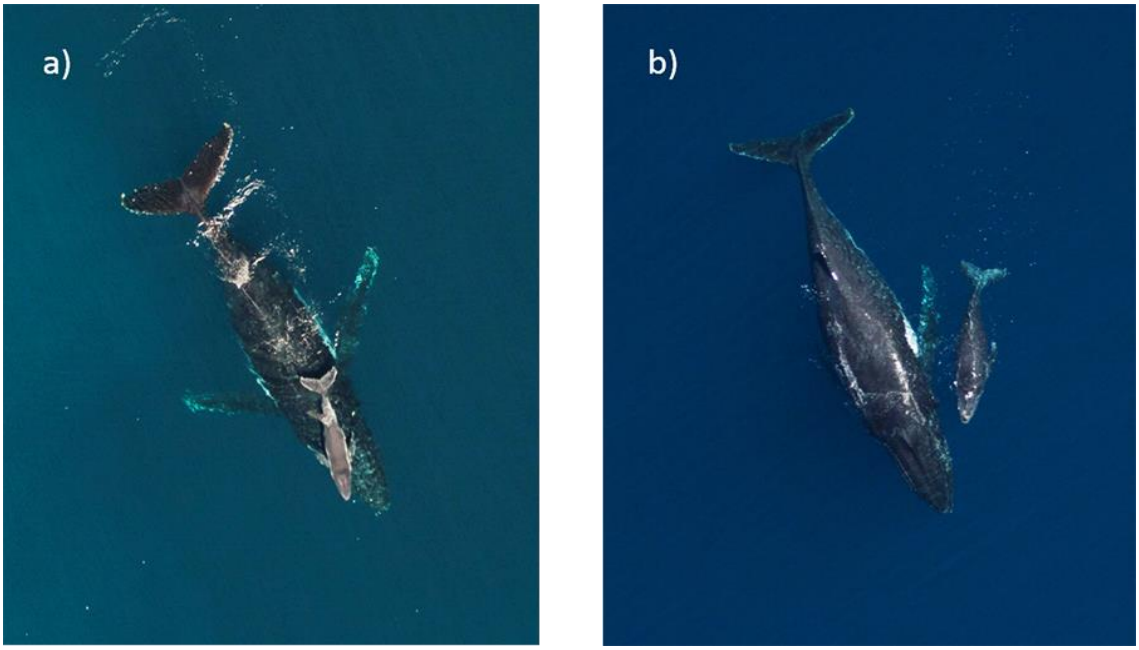

Figure 4.3. Representative images of a) neonate humpback whale calf with mother, displaying the light grey colour and body size approx. 1/3 of mother and b) post-neonate calf with mother, displaying the dark pigment and body size >1/3 of mother body length.

4.3.3 Data analysis

An estimate of the minimum daily relative abundance (uncorrected for availability and perception bias) of calves migrating northwards past North West Cape was calculated after Salgado Kent *et al.* (2012): the number of northbound calves sighted was multiplied by the mean migration speed of mother-calf groups (km/h) and the number of hours in a day (24), and divided by the latitudinal length of each survey (km). For migration speed, we used two estimates measured previously in the vicinity of North West Cape: 4.0 knots (7.4 km/h) (SE = 0.41, *n* = 14) from aerial observations of northbound mother-calf groups (Chittleborough, 1953) and 3.1 knots (5.65 km/h) (SE = 0.33, *n* = 44) from boat-based focal follows of northbound humpback whale groups (Salgado Kent et al., 2012).

An estimate of the minimum annual relative calf abundance (i.e. the number of calves passing through the study area during the northbound migration each season) was calculated by averaging the minimum daily relative abundance (calculated above) and multiplying by the number of days over which calving was observed: 34 d in 2013 (23 July - 25 Aug 2013); 47 d in 2015 (3 July - 19 Aug 2015). In 2015 flights were initiated earlier in the season (3 July) to investigate whether the calving period extended beyond that observed in 2013. As only a small number of calves were sighted in early July in 2015 (one on July 3 and another on July 7), and spotter pilots working in the area reported that these early sightings were sporadic, we used two calving periods in our 2015 abundance estimates: 47 d (3 July - 19 Aug) and 28 d (22 July - 19 Aug), and present both for comparison.

4.4 Results

In 2013, ten flights of 0.8 - 4.7 h duration (mean = 2.9 h) were carried out between 23 July and 25 August, covering a coastline distance between 16.5 and 47.4 km (table 4.1). The number of calves photographed each flight ranged from 1 to 10, with 41 calves sighted in total (table 4.1). Most of the calves (85%), were classified as neonates, while 15% were classified as post-neonates (table 4.1). Almost all neonate calves (97%) were travelling northwards; 17% of the post-neonates were travelling northwards and 83% were milling (table 4.1). Travel speed had an impact on the abundance estimates with a mean of 18.3 calves per day at a migration speed of 7.4 km/h and 14.0 calves per day at 5.65 km/h (figure 4.4).

In 2015, 11 flights of 0.7 - 3.2 h duration (mean = 1.8 h) were carried out between 3 July and 19 August, covering a coastline distance between 10.0 and 107.4 km (table 4.2). Between 1 and 15 calves were photographed each flight, with 69 calves sighted in total (table 4.2). Ninety-four percent of the calves were classified as neonates and 5.8% as post-neonates (table 4.2). Almost all neonate calves (95.4%) were travelling northwards while only half of the post-neonates were doing so, and the other half

were milling (table 4.2). As above, travel speed used in the calculation had an impact on the abundance estimates, with a mean of 22.6 calves per day at a migration speed of 7.4 km/h and 17.4 calves per day at 5.65 km/h (figure 4.4). Truncating the 2015 data set to a 34 day calving period, rather than a 47 day calving period, did not greatly affect the mean daily calf abundance (figure 4.4).

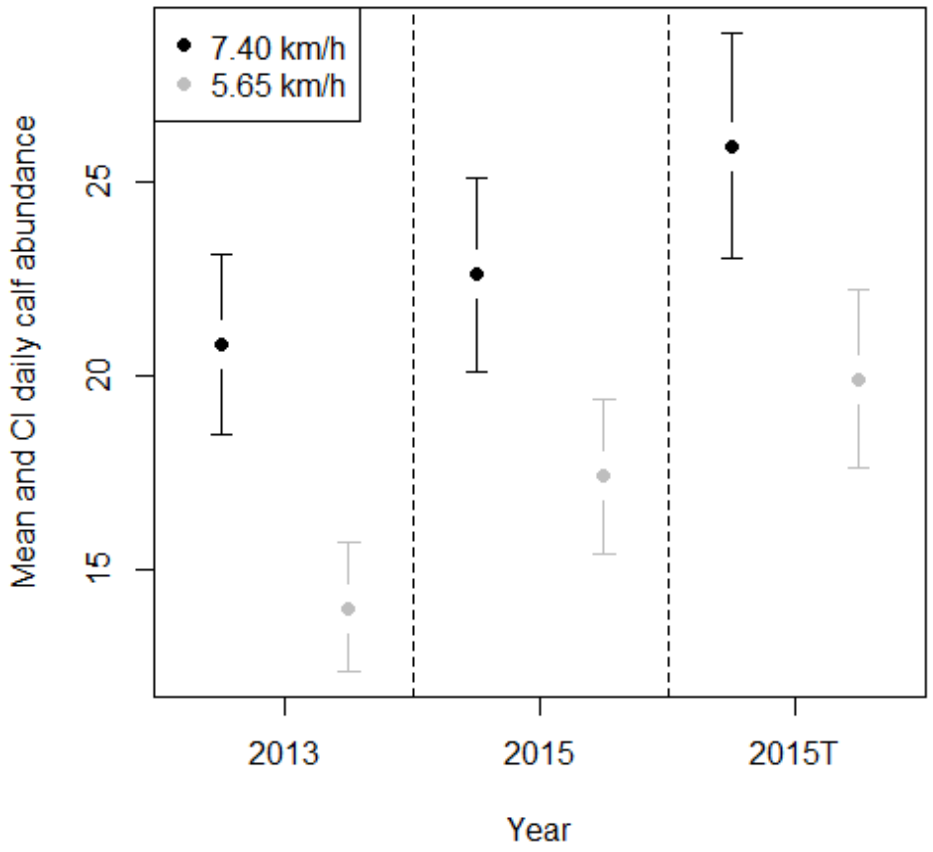

Figure 4.4. Minimum relative daily abundance of humpback whale calves along North West Cape calculated using a speed of 7.4 km/h (black) & 5.6 km/h (grey). Shown are the mean values and 95% confidence intervals in 2013, 2015 (using a calving period of 47 d) and 2015T (using a truncated calving period of 28 d).

The annual minimum relative calf abundance (i.e. the estimated minimum number of northbound calves born along or south of North West Cape) was affected by both travel speed and truncating the data set (figure 4.5). In 2013, annual calf abundance estimates were 603 and 463 at migration speeds of 7.4 km/h and 5.65 km/h, respectively, while in 2015 they were 1,063 and 817 using the full data set and 725 and 557 using the truncated data set.

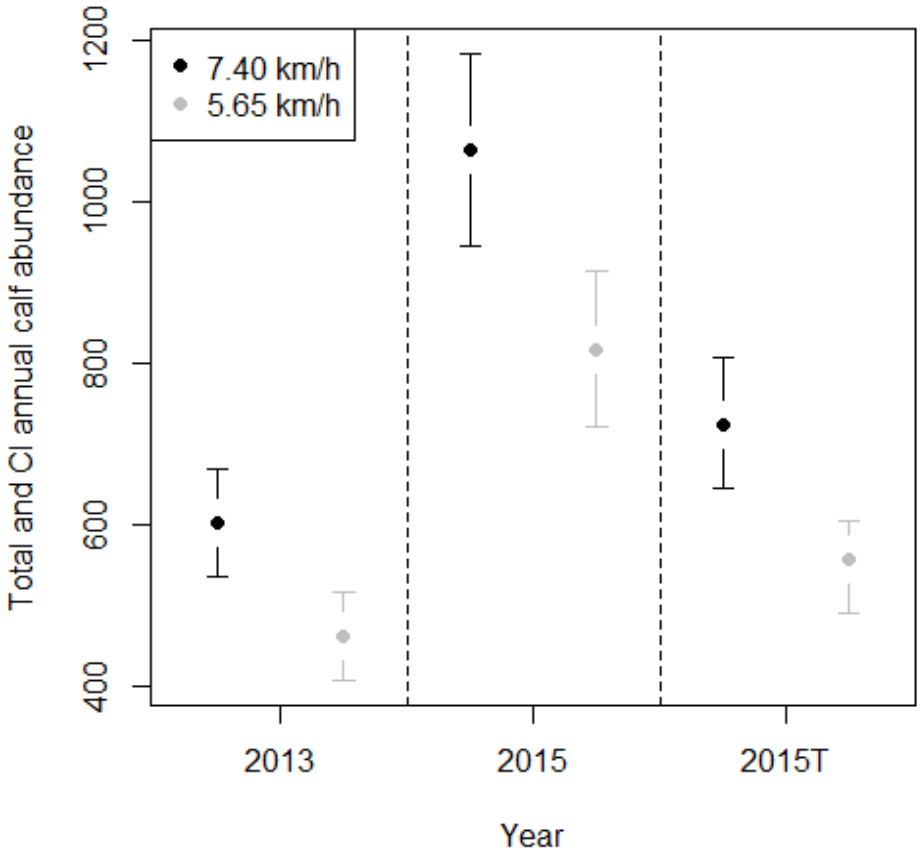

Figure 4.5. Minimum relative annual abundance of humpback whale calves along North West Cape calculated using a speed of 7.4 km/h (black) & 5.65 km/h (grey). Shown are the total values and 95% confidence intervals for 2013, 2015 (using a calving period of 47 d) and 2015T (using a truncated calving period of 28 d).

To quantify the importance of these findings at the population level, we compared our annual minimum relative abundance estimates with the expected annual calf production for the BSD population. The most recent estimate of the BSD population

was 19,264 (17,553 - 24,012) in 2012 (IWC, 2014). Based on an annual increase of between 10.15% (Bannister and Hedley, 2001) and 13% (Salgado Kent et al., 2012), the BSD population was likely to have been 21,200 - 21,800 in 2013 and 25,700 - 27,800 in 2015. Assuming that an estimated 31.6% of the BSD population are mature females (Chittleborough, 1965) with an average birth rate of 0.37 calves per year (Chittleborough, 1965), 2,481 - 2,545 calves were likely to have been born in 2013 and 3,010 - 3,250 in 2015. Our minimum relative abundance estimates of between 463 and 603 calves in 2013 represent 18.2% - 24.3% of the expected number of calves in the population that year. For 2015, the abundance estimates of 817 - 1,063 with a 47 d calving period and 557 - 725 with a 28 d calving period (table 4.3) represent 25.1% - 35.5% and 17.1% - 24.1% of the expected number of calves, respectively. Assuming that the BSD population estimates are accurate, and using the conservative calving period of 28 d in 2015, these results indicate that a minimum of approximately 20% (17.1% - 24.3%) of the calves of the BSD population are likely to be born along, or south of, North West Cape.

Table 4.3. Estimated daily and annual minimum relative abundance of humpback whale calves migrating northwards along North West Cape, Western Australia, in 2013 and 2015. Confidence intervals of the abundance estimates are reported in parentheses. The estimated annual calf abundance was calculated by multiplying the mean daily calf abundance by the duration of the aerial survey program (an estimate of the calving period).

Year	Migration speed (km h^{-1})	Mean daily minimum relative calf abundance	Date first flight	Date last flight	Duration of study (d)	Estimated annual minimum relative calf abundance
2013	7.4	18.3 (16.2 - 20.3)	23 July	25 August	33	603 (536 - 670)
2013	5.65	14.0 (12.4 - 15.7)	23 July	25 August	33	463 (409 - 517)
2015	7.4	22.6 (20.1 - 25.1)	03 July	19 August	47	1063 (946 - 1182)
2015	5.65	17.4 (15.4 - 19.4)	03 July	19 August	47	817 (722 - 913)
2015	7.4	25.9 (23.0 - 28.8)	22 July	19 August	28	725 (645 - 806)
2015	5.65	19.9 (17.6 - 22.2)	22 July	19 August	28	557 (492 - 606)

The calf groups sighted along North West Cape were distributed along a narrow corridor that followed the contour of the seaward edge of the fringing reef (figure 4.6), in waters between 15 and 129 m depth. The mean (±SD) water depth of calf

group sightings was 45 ± 20 m in 2013 and 40 ± 14 m in 2015, with 88% and 96% of sightings occurring in water depths of ≤60 m in 2013 and 2015, respectively. No calf groups were sighted along the track line that followed the 200 m depth contour (~5 - 10 km seaward of the reef edge). Groups sighted along this offshore track were far more numerous than groups sighted along the inshore track, however, they were not quantified or recorded in a systematic manner, as groups not containing calves were beyond the scope of this research. Some calf groups in 2015 may have been positioned between search tracks (~5 - 10 km apart), and thus not sighted. However, the locations of the calf sightings in 2013 (sighted during search tracks flown perpendicular to the coastline, rather than parallel as in 2015) indicate that these numbers would likely be minimal.

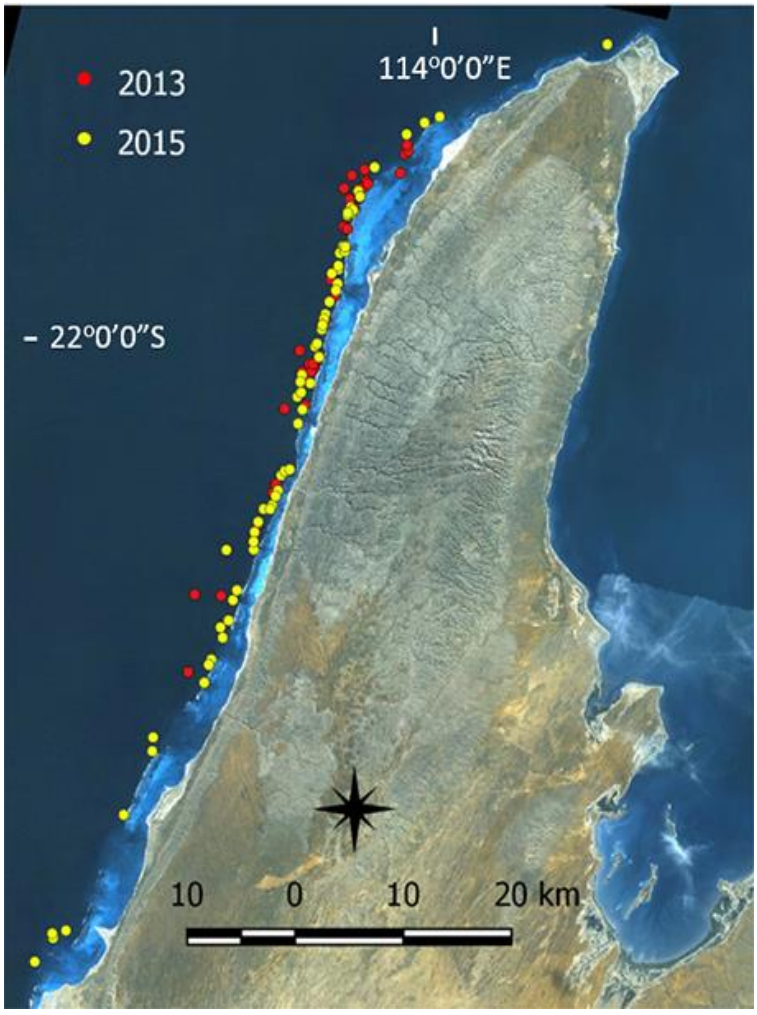

Figure 4.6. Locations of humpback whale calf groups along North West Cape during July and August 2013 (red points) and 2015 (yellow points).

4.5 Discussion

Our observations of large numbers (approx. 20% of the annual calf production of the BSD population) of humpback whale calves along North West Cape indicate that the calving areas of the BSD population are more extensive than currently recognised. The light colour, small size, and northward movement of the majority of the calves indicates that they were born near, or south of, North West Cape during migration. The presence of larger post-neonate calves, although low in numbers, suggests that some calves were born substantially further to the south of North West Cape. Our results indicate that the calving range of the BSD population extends at least 1,400 km along the migratory corridor from Camden Sound (15^{o}S) to Point Cloates (22^{o}43'S). This expands the currently recognised calving range by 1,000 km to the south west. These results also provide key information about the distribution and abundance of calves in this part of their wintering grounds and provides important information with which to manage this iconic species.

Observations of neonate calves as far south as Albany and in the Point Cloates region in 1952 (Chittleborough, 1953), lead Chittleborough (1965) to suggest that parturition in the BSD population could occur at any location on the migratory path along the Western Australian coast. Despite these observations, the currently recognised calving areas of this population is documented to lie between 15^{o}S - 18^{o}S in the Southern Kimberley (Department of the Environment and Heritage, 2005). Our observations of high numbers of neonate calves along North West Cape support Chittleborough's suggestion of widespread parturition along the migratory corridor. The paucity of reports of neonate calves from southern Western Australia, however, along with the high numbers of neonates recorded along North West Cape in this study, indicates that parturition is uncommon along the higher latitudes of the Western Australian coast and more frequent in the lower latitudes. A similar scenario occurs on the east coast of Australia, where important calving grounds have been described for the Breeding Stock E population (BSE) in the waters of the Great

Barrier Reef at ~ 20°S, but northbound newborn calves have also been sighted further south, off Moreton Island (27°S) (Paterson and Paterson, 1984, Paterson and Paterson, 1989). It is not clear if there is any location along the western Australian migratory corridor where parturition begins to occur more frequently, but it is clear that by the latitude of 22°43'S (Point Cloates) parturition is fairly common.

The frequency and colour range of the calves in this study (many light grey calves and few calves with adult colours) suggests that the majority of the calves observed at North West Cape are very young, however, some may be up to four weeks old (Kaufman and Forestell, 2006). At an average swim speed of 7.4 km/h (Chittleborough, 1953), calves can theoretically travel distances of up to 180 km each day. Thus, some of the older calves observed in this study may have been born a substantial distance south of North West Cape. Alternatively, the darkening of pigment from light grey to adult colours may occur over shorter time scales.

The recognised calving grounds, between Camden Sound and Broome, were identified in 1997 (Jenner et al., 2001) at a time when the BSD population was recovering from commercial whaling (Bannister, 1964, Chittleborough, 1965). This population has been increasing at a rate of 10% - 13% each year (Bannister and Hedley, 2001, Salgado Kent et al., 2012) and between 1997 and 2012, the population increased from less than approximately 10,000 to greater than 20,000 (Hedley et al., 2011, Salgado Kent et al., 2012, IWC, 2014). During this time, there has been no comprehensive survey along the West Australian coast to identify or describe the calving areas. It is not clear whether the calving range of this population is now expanding to that of the pre-whaling days or if calf numbers are now reaching sufficient levels to be observed more readily throughout their entire range. Regardless, it is evident that parturition in the BSD population occurs along an extended area of the migratory corridor, rather than a specific localised calving area. Such widespread calving activity may similarly be a feature of other populations

around the globe, and may become more apparent as their numbers also continue to increase.

The mother-calf groups travelling northwards along North West Cape were located very close to the reef edge, while groups without calves travelled further offshore. Such habitat segregation during migration has been suggested for the BSD population (Jenner et al., 2001) and described in other humpback whale populations (Ersts and Rosenbaum, 2003, Craig et al., 2014) and other baleen whales including gray whales (*Eschrichtius robustus*) (Jones and Swartz, 2009) and southern right whales (*Eubalaena australis*) (Rayment et al., 2015, Elwen and Best, 2004a). Possible reasons for mothers calving in shallow waters close to the coast include preference for calm, protected waters (Ersts and Rosenbaum, 2003, Elwen and Best, 2004a), predator avoidance (Ford and Reeves, 2008, Pitman et al., 2014) and intimidation (Heithaus et al., 2008, Wirsing et al., 2008), and avoidance of harassment by male conspecifics (Craig et al., 2014). Predation by killer whales (*Orcinus orca*) in the region appears to be particularly relevant to this population as, although killer whales typically prey on first season calves (Mehta et al., 2007) and sometimes subadults (Saulitis et al., 2015), the killer whales along North West Cape appear to prey mostly on neonate humpback whale calves (Pitman et al., 2014). In fact, predation pressure from killer whales along the Western Australian coast is thought to be higher than anywhere else around the globe, with a minimum of 100 humpback whale calves estimated to be taken by killer whales south of North West Cape each year.[4] An extended calving range along the migratory corridor, rather than a concentrated aggregation area, would have the advantage of reducing predictability of whale occurrence and thus potentially reducing predation pressure.

Until recently, it was believed that the majority of the BSD population travelled to the Kimberley calving grounds before terminating their northward migration and

[4]Personal communication from Robert L. Pitman, Southwest Fisheries Science Centre, National Marine Fisheries Service, 8901 La Jolla Shores Dr., La Jolla, California 92037 USA, August 2016.

turning southwards to return to their feeding grounds (Jenner et al., 2001). However, a recent satellite tagging study demonstrated that some adults terminate their migration a substantial distance (850 km) south of this northernmost destination (Double et al., 2012). We suggest that this may also be the case for calves born south of the recognised calving grounds, with those finding suitable habitat near their birthing location perhaps not travelling to the Kimberley coast. This would presumably represent a substantial energy savings to mothers and their calves. Although speculative, this is supported by observations of mothers with young calves resting in Exmouth Gulf[5] and the nearby Onslow region (authors' personal observation) during August. Although Exmouth Gulf is a recognised resting and nursing area for mother-calf pairs (Chittleborough, 1953, Department of the Environment and Heritage, 2005), the calves resting here are believed to be older southbound calves, born earlier in the season in the Kimberley calving grounds (Jenner et al., 2001). Given that parturition in the BSD humpback whales occurs between June and October (Chittleborough, 1958), it is feasible that Exmouth Gulf and other suitable locations along the coast are used as nursery areas by both young northbound calves and older southbound calves. Adults that travel to the most northerly destinations, such as the Kimberley, may need to replenish their energy stores before reaching their Antarctic feeding grounds. Recent research has shown that some individuals from the BSD population deviate westwards from the typical migratory pathway along the Western Australian coast during their southern migration (Double et al., 2010). It is possible that this alternative migratory route leads to a destination that provides feeding opportunities north of the known feeding grounds in Antarctic waters (Eisenmann et al., 2016, Owen et al., 2017).

Our calf abundance estimates were based on opportunistic data and represent minimum relative abundance, as the *ad hoc* nature of the study did not allow for calculation of availability (detectability) or perception bias. These analyses provide a

[5] Personal communication from Eric Roulston, Chief Pilot, Norwest Air Work, PO Box 909 Exmouth, 6707 Western Australia, Australia, August 2013.

very useful preliminary evaluation, designed to stimulate further research, but given the limitations and gaps in knowledge, our abundance estimates should be considered approximations only.

One key variable affecting our estimates was calf migration speed. Although the speeds used here are faster than that of young calves recorded in other areas around the world (e.g. 4.4 km/h in the Hawaiian calving grounds (Cartwright and Sullivan, 2009b); 3.6 km/h along the Eastern Australian coast (Noad and Cato, 2007), they were considered more appropriate, as they were taken from published studies of humpback whales observed in the same area as our study and during the same time period (during the northern migration). Of the two speeds we used, we believe that the migration speed recorded by Chittleborough (1953) is likely the most representative as it was observed on individuals at the same developmental stage as those in our study. This is important for neonate baleen whale calves, which are known to undergo a period of rapid and persistent travel following birth that begins to slow as they approach one month of age (Thomas and Taber, 1984, Cartwright and Sullivan, 2009b). As expected, this migration speed is slower than that of groups without calves (9.0 km/h) recorded in the same area (Chittleborough 1953). The seemingly fast migration speed may be due to the unique conditions found off North West Cape. Here, the waters lie over the narrowest section of continental shelf along the Western Australian coast and are flanked by a fringing coral reef that acts as an inshore barrier to humpback whale movement. In this area the majority of the population travel close to the shore (Department of the Environment and Heritage, 2005), but are unable to access the shallow waters of the lagoon. It is possible that the thinning of the migratory corridor against the reef edge influences migration speed, particularly for mother-calf groups trying to avoid predation.

Uncertainty about the duration of the calving period also introduced potential errors into the abundance estimations for the total calving period, with the value increasing significantly when the calving period was not truncated. In this study, we have taken

a cautious approach in our abundance estimations by focusing on the truncated calving period and including only calves that were travelling.

We acknowledge that our calculation of the proportion of calves that are born along, or south of, North West Cape is based on the assumption that the values of mature female abundance and average birth rate reported by Chittleborough (1965) are stable. Given that these values may have changed, particularly after the cessation of commercial whaling, our calculations are again considered approximations only and designed to put our abundance estimates in the context of the total BSD population and thus stimulate further study.

Regardless of the above limitations, our abundance estimates clearly demonstrate that a substantial number of humpback whale calves are born south of the recognised calving grounds along the Kimberley coast, and highlight the need to investigate the full extent of the calving grounds along the Western Australian coast. These abundance estimates could be improved in the future by systematic surveys over the entire calving period using distance sampling techniques; determination of calf speed and behaviour throughout their early development; further information on killer whale predation along the Western Australian coast; and an up to date assessment of the entire BSD population.

4.6 Acknowledgements

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Chapter 5

General Discussion

Each year humpback whales (*Megaptera novaeangliae*) migrate tens of thousands of kilometres from high latitude feeding grounds to low latitude breeding grounds in the longest known migration of all mammals (Rasmussen et al., 2007). Although the reasons for this vast annual migration are not well understood (Corkeron and Connor, 1999, Clapham, 2001), it requires a suite of morphological and physiological adaptations that enable survival and reproduction during long periods of fasting. The energetic challenge of simultaneous lactation and fasting is so great that it is achieved by only a select few large mammals such as bears, large phocid seals and baleen whales (Oftedal, 1993). The extreme migration of humpback whales makes them an ideal species for the examination of long-distance migration and the energetic strategies that make it possible.

5.1 New insights presented in this thesis

Thus far, energetic strategies of long-distance migration have been poorly studied as the large body size of baleen whales and their aquatic existence make sampling difficult. However, this thesis utilised long forgotten unique datasets from the commercial whaling era to quantify energy stores of both humpback and sperm whales - two large cetaceans with differing life histories. To fuel their annual migration, capital breeding humpback whales were found to store 32-75% more body lipid than income breeding sperm whales (*Physeter macrocephalus*). For the humpback whales, pregnant females stored 26% more energy than non-pregnant females, and 37% more energy than males, illustrating the high energetic demands of reproduction. Furthermore, pregnant females arriving along the western

Australian coast later had larger energy stores than those that arrived earlier, presumably from feeding for longer durations in Antarctic waters.

In this thesis, photogrammetric methods were used on free-swimming humpback whales to identify energy storage sites that can be reliably used as an index for body condition. These energy storage sites were used to quantify annual rates of cow body condition decline and calf growth, demonstrating annual variations in maternal investment. The body condition of lactating cows was found to decline at a rate of 0.36 cm/day in 2013 and 0.65 cm/day in 2015 while calves grew at a rate of ~3.1 cm/day in 2013 and 2.4 cm/day in 2015 during the first six weeks of lactation. This is the first time that annual differences in maternal investment have been quantified for humpback whales.

Photogrammetric methods were also used to identify calves observed off North West Cape as neonates, establishing that they were born nearby to the region. The associated behavioural data and survey details illustrated that approximately 20% of the expected number of calves in the BSD population were born at least 1000 km south of currently recognised calving grounds. This provided strong evidence that the BSD calving areas are more extensive than those currently recognised.

The results of this thesis have provided new insights into migratory behaviour of humpback whales and the energetic tactics that have enabled them to travel vast distances each year between their high latitude feeding grounds and low latitude breeding grounds. Below, I discuss the main findings in a broad ecological context, with particular focus on the energetic strategies used by long-distance migrants, and the implications of calving areas extending along migratory corridors.

5.2 Life history strategy and body size

Capital and income breeders use different life history strategies to acquire and allocate resources in a way that optimises survival and reproduction (Stearns, 1992, Jönsson, 1997). Capital breeders use stored energy for survival and reproduction, while income breeders use energy accrued on a continual basis (Stearns, 1992, Jönsson, 1997). In chapter 2 of this thesis, I was able to explore these different strategies by quantifying total body lipid stores of two similar sized cetaceans with different life histories. I illustrated that capital breeding humpback whales stored 32-75% more energy than income breeding sperm whales, thus highlighting the importance of large energy stores for capital breeders who finance the cost of both reproduction and survival with stored energy whilst in their breeding grounds.

I was also able to demonstrate the advantages of large body size for capital breeders in chapter 2, by quantifying the positive relationship between body length and energy stores for both sperm and humpback whales. For example, the equations I developed illustrate that 12m male sperm whales store approximately 415 litres of lipid per metre of body length, while 14m male sperm whales store ~540 litres (Irvine et al., 2017b). In comparison, 12m and 14m male humpback whales store ~620 and ~720 litres of lipid per metre of body length respectively (Irvine et al., 2017b). In mammals, body size affects metabolic costs as well as energy storage capabilities. Large individuals have lower relative energetic costs than small individuals as maintenance metabolism is proportional to surface area ($\sim mass^{0.75}$) whilst energy stores are proportional to body size or volume ($mass^{1.0}$) (Brodie, 1975, Calder, 1984, Millar and Hickling, 1990). As such, large individuals have relatively low metabolic costs and relatively high energy storage potential in comparison to smaller individuals (Brodie, 1975).

Large energy stores are crucial for capital breeders as they must carry sufficient energy to sustain them during periods of fasting when food resources are scarce or

non-existent. Larger animals are capable of longer fasts due to their larger energy storage capabilities (Lindstedt and Boyce, 1985, Millar and Hickling, 1990). Those capable of long-endurance fasting are able to de-couple feeding and breeding activities (Oftedal, 1993) and utilise different habitats that are optimal for different lifecycle activities. For baleen whales, this has enabled feeding in productive polar waters and breeding in oligotrophic tropical waters (Lockyer and Brown, 1981), while for pinnipeds it has enabled a lifecycle that consists of discrete marine and terrestrial components i.e. feeding in the marine environment and breeding (and moulting) on land (McMahon et al., 2000).

The accumulation of large energy reserves requires the availability of abundant food resources. However the large energy storage capabilities of large animals negates the need for immediate energy intake and thus allows time for searching and accumulation. The capital breeding strategy is thus beneficial in areas of patchy and widely dispersed prey (Costa, 1991), such as that of Antarctic krill (*Euphausia superba*) in the Southern Ocean (Tarling et al., 2009, Jarvis et al., 2010, Cox et al., 2011). Large marine mammals are particularly suited to capital breeding as their relatively low cost of locomotion enables them to travel large distances in search of food and their large body size enables them to store the large energy reserves (Brodie, 1975, Calder, 1984) required for long-endurance fasting.

Income breeding strategists in contrast, accrue energy on a regular basis to fuel reproduction. This strategy is generally suited to smaller mammals that have high metabolic costs and relatively low energy storage capabilities. Amongst marine mammals, this strategy is used by the odontocetes, the otariid seals and the smaller phocid seals (<100 kg) (Oftedal, 1997, Oftedal, 2000). Income breeding relies on predictable and regular food resources as daily food intake must be increased to match daily energy demands. For example, the daily energy demand of income breeding sea otters (*Enhydra lutris*) increases by 96% during lactation (Thometz et al., 2014), whilst the demand for capital breeding elephant seals (*Mirounga*

angustirostris) increases by only 12% (Costa, 1993). However, the strategy of regular energetic income enables longer lactation periods and thus relatively larger offspring with higher lean mass (Costa, 1991). Some species use a mixture of capital breeding and income breeding strategies, supplementing milk production with food intake when localised prey resources are available e.g. Weddell seals (*Leptonychotes weddellii*) (Wheatley et al., 2008).

The relationships I quantified in chapter 2 of this thesis between body length and energy stores also enabled me to identify cohorts in the population that may be at risk of depleting their energy stores during the annual humpback whale migration. More specifically, my results indicated that smaller (shorter) individuals, with their low relative energy stores, are more vulnerable to higher levels of energetic stress during the migration fast. Thus, they may be more prone than larger animals to exhausting their energy stores before returning to their feeding grounds. Small juveniles and small maternal females are particularly vulnerable to energetic stress during a migration fast, as they must finance the high costs of growth and lactation, respectively, whilst in the breeding grounds (Lockyer, 1981b, Fortune et al., 2013). Juveniles are one of the first cohorts to return to the feeding grounds to replenish their energy reserves (Chittleborough, 1965, Dawbin, 1997). However, their vulnerability to energy exhaustion during the migration fast appears to be evidenced in baleen whale stranding events, where they represent a high percentage of individuals stranding in an emaciated condition (e.g. Coughran et al., 2013).

Lactating females also have the highest energy costs of all cohorts (Lockyer, 1981b, Fortune et al., 2013), but unlike the juveniles, they remain in the breeding grounds to nurse their calves (Chittleborough, 1965, Dawbin, 1997). The quantification of energy stores in chapter 2 of this study demonstrated that larger pregnant females stored relatively higher energy reserves than smaller pregnant females, with small pregnant females (~12m) storing 730 litres of body lipid per metre of body length and larger pregnant females (~14m) storing 960 litres (Irvine et al., 2017b). As such,

small breeding females have less energy to finance reproduction than larger breeding females. These smaller females may either transfer less energy to their offspring, potentially affecting offspring growth (Arnbom et al., 1993, Christiansen et al., 2018), or invest the same energy as larger individuals at the cost of their own body condition (Fedak et al., 1996). For example, it has been estimated that physically mature fin whales (*Balaenoptera physalus*) expend a total of 19% of their total energy costs on gestation and lactation, whilst recently mature animals expend 26% (Lockyer, 1984). If these energy stores need replenishing, breeding females may be forced to depart from their breeding grounds early, thereby reducing the amount of time their calves receive a thermal advantage of residing in tropical waters.

5.3 Lactation and capital breeding

Capital breeding offers benefits to mammals in particular as offspring sustenance is provided in the form of lipid-rich milk (Oftedal, 1997) synthesised from energy reserves, rather than direct food transfer as in other groups such as birds (Pond, 1977). Offspring provisioning is thus independent of food intake, allowing energy stores to be accumulated over long time frames and large geographical areas prior to parturition (Costa, 1991). Combined with the large body size of baleen whales, this mammalian trait of lactation facilitates long-distance migration as large energy reserves can be accumulated in productive polar waters and then transported to oligotrophic tropical waters which are thermally favourable for young calves following parturition.

In mammals, large energy reserves enable efficient transfer of energy between mother and offspring, as energy during lactation is not required for locating, capturing and digesting prey. This enables short lactation periods and rapid offspring growth and dependency traits (Costa, 1993, Oftedal, 1997, Stephens et al., 2014) that are required when reproduction is synchronised with a short seasonal cycle. The strategy however, has high energetic costs for maternal females which much be

financed by large energy stores. I was able to quantify these large energy stores in chapter 2, demonstrating that pregnant females stored 26% and 37% more energy than resting females and males respectively, to satisfy the high energy demands of reproduction. These additional energy stores are consistent with those found for pregnant females of other baleen whale species such as fin and blue whales (Lockyer, 1981b).

5.4 Energy demands of lactation

The most demanding activity in the reproductive cycle for all mammals is lactation (Lockyer, 1981b, Fortune et al., 2013). Mammalian lactation requires 3 to 5 times more energy than gestation (Young, 1976). For mammals that lactate whilst fasting, the drain on energy reserves can be substantial, resulting in losses of up to 40% of initial body mass (Oftedal, 1993). In baleen whales, this energy loss is manifest in body shape, with lactating females being the leanest in the population and pregnant females being the widest (Perryman and Lynn, 2002, Miller et al., 2012).

In chapter 3 of this study, I used aerial photogrammetric techniques on free-swimming humpback whales to explore body shape and quantify the body condition decline of lactating females. By measuring relative widths at multiple locations along the body, at two different stages of migration, I identified that the location mid-way along the body is a dominant energy storage site that can be used as an index for estimating adult body condition. By using measurements from this location, I was able to illustrate that the width of lactating females decreased between 5 and 10% during the first 6 weeks of lactation.

The energy demands of mammalian offspring increase throughout pregnancy and lactation, with late lactation being the most costly period. During late lactation mammalian mothers require a daily increase of ~0.5 to 3 (average 1.65) times their maintenance costs to successfully wean offspring (Millar, 1977, Thometz et al.,

2014). The energy costs of these high demands are illustrated in the smallest marine mammal, the sea otter, which experiences high rates of adult mortality during late lactation due to severe depletion of energy reserves (Chinn et al., 2016). The high energy demands of late lactation were also illustrated in my thesis by the poor body condition of humpback whales who were likely feeding large calves that were near independence. These females had been in Antarctic feeding grounds prior to their return to breeding grounds, to wean their (~10.5 month old) calves, but their body condition was substantially poorer than that of lactating females sampled during the first 6 weeks of lactation. Their body shapes were extremely thin, with the widest part of the body being the head (at the location between the eyes). This thin body condition indicated that their energy demands could not be met by energy intake in the feeding grounds, and that they were and that they were likely energetically compromised. The good body condition of their calves (Body Condition Index (BCI) 50% = ~0.25) in comparison to that of their mothers (BCI 50% = ~0.16) may suggest that the mothers prioritised maternal care over their own individual energy needs. Although this is unusual in a long-lived species that is expected to maximise survival by reducing offspring investment in times of nutritional deficit (Hamel et al., 2010), it has also been observed in other marine mammal groups including right whales (Bradford et al., 2012, Fortune et al., 2013) and sea otters (Thometz et al., 2016). Although not well understood, it has been suggested that this may be the result of resource limitation at a time when the mother is already heavily invested in reproduction (Bradford et al., 2012). Whatever the reason, the inability to replenish energy stores before leaving the feeding grounds, and the resultant poor body condition, may have costs in terms of future reproductive success (Desprez et al., 2017). In some areas, humpback whales have been observed feeding during their southern migration (e.g. Stamation et al., 2007, Owen et al., 2017). Such supplementary feeding would provide an important energy boost prior to arrival in the polar feeding grounds. Although, this has not been observed in the BSD population, two tagged individuals have been recorded travelling to a location 1200

km west of their typical migration route during their southern migration, possibly to exploit temperate feeding areas (Double et al., 2010).

To accumulate the enormous energy reserves required for simultaneous fasting and lactation, pregnant baleen whales stay longer in the feeding grounds than other reproductive classes (Lockyer, 1981b, Dawbin, 1966). In Chapter 2 of this thesis, I demonstrated the benefits of extended durations in the feeding grounds, by showing that pregnant females that arrived later along the coast had larger energy stores than those that arrived earlier. This provides a benefit in terms of maximising the energy available for milk synthesis. However, extended residency in cold Antarctic waters has an energetic cost for both mothers and young calves (Rutishauser et al., 2004) by reducing the amount of time in thermally favourable breeding grounds during early lactation and calf development. This presents pregnant females with a pre-partum trade-off between staying in the feeding grounds to accumulate energy stores in preparation for lactation, or departing in time to allow parturition in tropical breeding grounds. A similar trade-off exists post-partum, with females either remaining in tropical breeding grounds to transfer energy stores to calves in a thermally favourable environment, or returning to cold Antarctic waters to replenish their own energy stores.

5.5 Maternal investment and calf growth

In chapter 3 of this thesis I used photogrammetric methods to quantify calf growth rates. My results illustrated that humpback whale calves grow from ~38% to ~47% of their mother's body length in the first 6 weeks of life, and to 63% of adult length at the time of weaning. This rapid growth rate is consistent with that of other baleen whales who have some of the most rapid offspring growth rates amongst all the mammals (Frazer and Huggett, 1974). Weights of baleen whale calves are known to increase more than 10-fold in their first year (Lockyer, 1981b), with lengths reaching up to 75% of adult body length by the time of weaning (Clapham et al., 1999, Fortune

et al., 2012). This body size is high in comparison to terrestrial mammals who reach an average of 37% of adult length at weaning (Millar, 1977).

As weaning size in marine mammals is known to influence subsequent survival (McMahon et al., 2000, McMahon et al., 2015), rapid growth rate is important for maximising offspring survival rates. Rapid growth during lactation may increase calf survival through various means such as improving swimming and diving capabilities (Thomas and Taber, 1984, Irvine et al., 2000), minimising predation (Ford and Reeves, 2008, Pitman et al., 2014), and increasing insulation for cold Antarctic waters (Rutishauser et al., 2004). Rapid calf growth has also been suggested as a tactic for speeding up mouth development, to optimize the foraging efficiency of juveniles at the time of weaning (Goldbogen et al., 2010, Fortune et al., 2012). It may also improve reproductive fitness through reducing the age at which sexual maturity is attained (Pontier et al., 1993).

5.6 Energy acquisition in a variable environment

By illustrating the decline in body condition of lactating females, chapter 3 of this thesis highlighted the energy drain associated with the rapid growth rate of the calves. This rate of cow body condition decline differed between years, as did the growth rate of the calves, indicating variation in both maternal energy reserves and maternal investment. Baleen whale body condition is known to fluctuate annually in response to environmentally mediated prey availability in the feeding grounds (Lockyer, 1986, Ichii et al., 1998) which has follow on effects to maternal investment (McMahon et al., 2017) and thus offspring development (Wheatley et al., 2006).

Although some humpback whale populations can access supplementary energy stores along their migratory corridor (Stamation et al., 2007), the BSD humpback whales rely on energy provided by Antarctic krill eaten over the austral summer for breeding and migration (Kawamura 1994). The abundance of Antarctic krill

(*Euphausia superba*) in the Southern Ocean fluctuates, both intra- and inter-annually (Priddle et al., 1988, Brierley et al., 1997, Loeb and Siegel, 1997, Murphy et al., 1998, Siegel et al., 1998, Hewitt et al., 2003). Such fluctuations have been shown to affect foraging trip duration, meal size, diet composition, adult body size, offspring provisioning rate, and ultimately breeding success in a range of krill predators (Croxall et al., 1999, Clarke et al., 2002, Trathan et al., 2007, Nicol et al., 2008). For example, a 4-fold decrease in krill biomass at South Georgia resulted in reduced breeding success in gentoo penguins (*Pygoscelis papua*), macaroni penguins (*Eudyptes chrysolophus*), black-browed albatross (*Diomedia melanophrys*), grey-headed albatross (*Thalassarche chrysostoma*) and Antarctic fur seals (*Arctocephalus gazella*) (Croxall et al., 1999), whilst a 3-fold decrease in krill biomass in the East Antarctic resulted in reduced breeding success of Adélie penguins (*Pygoscelis adeliae*) (Nicol et al., 2008).

The majority of information about the effects of variations in krill availability comes from central place foragers, such as penguins and seals, who return regularly to terrestrial breeding sites to feed their young. Less is known about wide ranging predators, such as the baleen whales, that have a greater ability to store energy and search for food over large areas and long time-frames. Baleen whales are able to track areas of high prey abundance (Tynan, 1999, Haug et al., 2002), and will switch prey where possible (Haug et al., 2002), but if food availability is affected over large scales, foraging success and body condition will be affected (Ichii et al., 1998).

In mammals, poor body condition is related to reduced body size, and increased juvenile mortality (Trites and Donnelly, 2003). For breeding females, poor body condition can result in reduced reproductive success (Guinet et al., 1998, McMahon et al., 2015, Seyboth et al., 2016), or high adult mortality rates (Le Boeuf et al., 2000, Fortune et al., 2013, Thometz et al., 2014). Alternatively, if females reproduce successfully, but can't recover from the energy deficit experienced through lactation, they may delay further reproduction until their energy stores have been replenished

(Lockyer, 1984, Proaktor et al., 2008, Fortune et al., 2013, Desprez et al., 2017). All of these outcomes influence population dynamics (Leaper et al., 2006, Proaktor et al., 2008, Fortune et al., 2013, Meyer-Gutbrod et al., 2015).

5.7 Humpback whale calving range

In chapter 4 of this thesis I used photogrammetric methods to identify neonate calves in an area considered to be outside the recognised calving grounds of the BSD population. I combined these observations with behavioural data and population assessments and estimated that a minimum of ~20% of the expected number of calves in the BSD population were born near, or south of, North West Cape. As this location is situated 1000 km southwest of the recognised calving grounds of the BSD humpback whale population, my findings provided evidence that the calving grounds are more extensive than those currently recognised.

As animal populations recover from declines and their numbers increase, they may undergo range expansions or re-colonise areas that were previously inhabited. In the case of the BSD humpback whales, observations of large numbers of neonate calves off North West Cape during the commercial whaling era (Chittleborough, 1953) demonstrate that the humpback whales are now re-colonising calving areas they used before their population declined.

These areas being re-colonised are closer to the feeding grounds, potentially providing mothers and their calves with a reduction in the cost of travel. Although speculative, such reductions in energy expenditure would enable mothers to allocate more of their finite energy stores to offspring development, and calves to allocate more energy to growth rather than to locomotion. However, this benefit would be offset by other energetic costs, such as heat production in cooler waters (Rutishauser et al., 2004) or predation avoidance (Pitman et al., 2014) in higher latitudes. Also,

calving over widely dispersed areas, rather than localised areas with high density, may offer reduced predation pressure from killer whales.

As calving areas expand, they may begin to overlap with areas of high anthropogenic activity. For humpback whales that prefer to migrate in shallow waters, these expansions will typically take place along or near to coastlines. The preference to breed in tropical waters between 21.1^{o}C and 28.3^{o}C (Rasmussen et al., 2007) results in many breeding areas being located in areas of high human use. For example, humpback whale breeding and calving grounds around the world include popular tourist destinations such as the Hawaiian Islands (Alison and Louis, 2000), the Great Barrier Reef (Smith et al., 2012), and Ningaloo Reef (Irvine, 2016). Such overlap could potentially result in disruptions to migratory behaviour if calm and protected waters for mothers and calves are in conflict with areas of high human use. In the terrestrial environment, numerous long-distance migrations around the globe have been lost from the consequences of high human population in migratory corridors. These include migrations of wildebeest (*Connochaetes taurinus*) in Namibia and South Africa, bison (*Bison bison*) in Canada and U.S.A and elephants in Kenya (*Loxodonta africana*) and India (*Elephas maximus*) (Berger, 2004). Long-distance migrants are particularly vulnerable to the effects of anthropogenic activity as they can be impacted at multiple locations, either singularly or cumulatively, along their migratory corridor (Berger, 2004, Moore, 2011).

In breeding grounds, baleen whale distribution is often segregated according to reproductive status. Males and non-reproductive females typically inhabit offshore waters, while maternal females and calves prefer shallow, protected waters around islands or in bays (Rice and Wolman, 1971, Ersts and Rosenbaum, 2003, Elwen and Best, 2004b, Rayment et al., 2015). Energetic benefits are conferred to mothers and calves in coastal waters through various mechanisms, including the minimisation of energy expenditure of calves in calm waters (Taber and Thomas, 1982), minimisation of predation pressure (Ford and Reeves, 2008, Pitman et al., 2014), and avoidance of

harassment by male conspecifics (Craig et al., 2014). However, coastal areas often experience high levels of human activity leading to potential overlap between critical habitat and anthropogenic disturbance. In Hawaiian breeding grounds for example, mother-calf groups have been found to avoid coastal areas with high levels of boat traffic, and use offshore waters instead (Cartwright et al., 2012). This exposes mothers and their calves to males actively seeking mating opportunities and results in a 30% increase in energy costs (Cartwright and Sullivan, 2009a).

For mammals, it has been suggested that behavioural modifications are potentially the most important tactic for minimising additional energy expenditure during reproduction (Gittleman and Thompson, 1988). Marine mammals use several strategies to conserve energy. For example, lactating elephant seals minimise energy expenditure by sleeping for much of the lactation period and remaining very close to their birthing sites for the entire lactation period (Gittleman and Thompson, 1988). Humpback whales have a series of resting areas located along their migratory corridor (Bannister, 1994, Jenner et al., 2001), where mother-calf pairs spend long periods of time resting in shallow, protected waters on their migration to the feeding grounds. Resting in warm waters allows mothers to conserve energy for lactation and calves to use energy for growth rather than for travel or heat production in cooler waters.

Areas with high levels of anthropogenic activity may disrupt the balance between energy expenditure and energy conservation required by capital breeding marine mammals in their breeding grounds (Braithwaite et al., 2015). For example, animals may change their activity levels or behaviour when exposed to disturbance, such as increasing swimming speeds or exhibiting avoidance behaviours (Corkeron, 1995, Stamation et al., 2009), with mothers and calves being the most sensitive to anthropogenic disturbance (Stamation et al., 2009). Maternal females are particularly vulnerable to the energetic consequences of disruptions as they must sustain both themselves and their suckling calves with their finite cache of energy

stores. Energy conservation strategies are important during the period of simultaneous lactation and fasting as they maximise the energy available for transfer to offspring. This is particularly important during the early stages of development when the calves are small and totally dependent on their mother's energy stores for nutrition (Lindström, 1999).

The results of this thesis highlight the need for monitoring the location and extent of calving areas as baleen whales recover from over-exploitation during the commercial whaling era last century. This is critical for identifying areas where potential conflicts with anthropogenic activity may occur, particularly in popular areas such as coastlines or coral reefs.

5.8 Why do baleen whales migrate?

The migrations of humpback whales, and most baleen whale species, are conspicuous and well-known annual events (Lockyer and Brown, 1981), however the drivers of these long-distance movements are not well understood. Unlike many terrestrial mammals, baleen whales do not migrate to follow food resources (Avgar et al., 2014), but instead move away from highly productive feeding areas into oligotrophic breeding areas. Unlike other marine mammals, such as pinnipeds, they do not have a physiological need to move to terrestrial locations to find mates, suckle their young, or to moult. Thus, the question of why baleen whales move from areas of energy intake to areas of energy expenditure is the subject of much discussion.

Currently, the most well accepted explanations for these migrations (Corkeron and Connor, 1999, Clapham, 2001) are increased calf growth and survival through energy conservation in warm, calm waters (Norris, 1967, Clapham, 2001), and predator avoidance, particularly for newborn calves, by moving away from high abundances of killer whales at high latitudes (Corkeron and Connor, 1999). The results of chapters 3

and 4 of this thesis provide some further insights into the reasons for these long-distance migrations.

The pattern of rapid somatic growth demonstrated in Chapter 3 of this thesis is typical of many baleen whale calves (Lockyer, 1981b, Best and Ruther, 1992, Perryman and Lynn, 2002, Fortune et al., 2012) and supports both the energy conservation hypothesis of Clapham (2001) and the predator avoidance hypothesis of Corkeron and Connor (1999). Rapid growth is facilitated in warm waters as energy can be allocated to calf growth and development, rather than to heat production. This maximises calf body size and thus reproductive success (Clapham, 2001). Rapid growth also supports the predator avoidance theory, as larger and stronger calves have more developed swimming capabilities (Taber and Thomas, 1982) and are thus less vulnerable to predation (Ford and Reeves, 2008). This tactic of minimising neonate predation to maximise offspring survival is also used by terrestrial mammals such as bighorn sheep (*Ovis canadensis*) (Festa-Bianchet, 1988) and caribou (*Rangifer tarandus*) (Heard et al., 1996).

The consistent northward movement of neonate calves and their mothers that I observed in chapter 4 of this thesis also supports both theories on the motives for whale migration. This northward movement is both away from high latitudes where predators occur (Pitman et al., 2014), and towards warmer waters where energy may be conserved (Norris, 1967). It is not clear however, how far north the calves in this study travelled and it is therefore difficult to draw any definite conclusions. In future research, the attachment of satellite tracking devices to establish long-range movements of mothers and calves would assist in clarification.

The fast travel speed of the neonates in the North West Cape area, that was observed in chapter 4 (authors' personal observation) and documented by Chittleborough (1953), is typical of the period of rapid travel reported during early baleen whale development (Thomas and Taber, 1984, Cartwright and Sullivan,

2009b). It has been suggested that this rapid travel is a tactic of developing swimming capabilities (Taber and Thomas, 1982), for the young calves when they are small and weak and at their most vulnerable stage (Gabriele et al., 2001). This fast travel speed thus supports the predator avoidance theory.

In contrast, the energy conservation hypothesis of Norris (1967) and Clapham (2001) is supported by the results of Rasmussen et al (2007) who found that global breeding areas are driven by water temperature rather than latitude. In addition, Clapham (2001) argues that the predator avoidance hypothesis is flawed due to i) the presence of killer whales in tropical waters but very little interaction between killer whales and humpback whales in breeding grounds and ii) a lack of any adaptive traits to impede killer whale predation such as social structure or behavioural modifications that other species with high predation pressure exhibit. However, in breeding grounds along the Western Australian coast, interactions between killer whales and humpback whales are common, with neonate calves being the primary target for predation (Pitman et al., 2014). In addition, humpback whales in this area exhibit several behavioural modifications to minimise predation such as male escorts helping mothers defend calves against killer whale attacks (Pitman et al., 2014) and low level vocalisations between mothers and calves so as not to attract predatory attention (Videsen et al., 2017).

There is increasing recognition that the benefits of migration may be multi-faceted (Avgar et al., 2014). The results of my thesis support this, with the observations of rapid calf growth and consistent northward movement of neonate calves supporting both of the most accepted theories for baleen whale migration. The warm waters of the breeding grounds provide a thermally favourable environment for rapid calf growth and development, which leads to large body size and thus lower predation pressure from killer whales (Pitman et al., 2014).

5.9 Photogrammetry as a tool for marine mammal studies

Whales, in particular baleen whales, are extremely large animals that live exclusively in an aquatic environment, making them very difficult to access and impractical to capture for measurement. Other marine mammals, such as seals, are much smaller animals with a terrestrial component in their lifecycle that enables them to be accessed for sampling. As a result, much of the knowledge about marine mammal energetics has come from research on seals (e.g. Worthy, 1987, Costa, 1993, Hindell and Slip, 1997, Mellish et al., 1999, Wheatley et al., 2006, McMahon et al., 2017). This has been informative for whale research given that phocid and otariid seals have a large size range and have adopted both capital and income breeding strategies, generally related to body size.

Studies of whale energetics have mostly relied on data from commercial hunting or stranding events. These extensive data sets from the historical whaling era, including those that provide the data source for the analysis in Chapter 2 (Irvine et al., 2017b) have given us valuable insights into cetacean energetics. However lethal sampling methods are not acceptable in the modern era and new techniques are required. Photogrammetry is a non-invasive technique that has been used on a wide range of species to measure a variety of morphological traits. This method is applicable to both terrestrial and marine organisms and is particularly suited to species that are difficult to access or impractical to capture, for example large ungulates (Berger, 2012) and whale sharks (*Rhincodon typus*) (Rohner et al., 2011, Sequeira et al., 2016). In cetacean studies, the technique has been used intermittently since the 1970's (e.g. Whitehead and Payne, 1976, Sumich, 1986, Best and Ruther, 1992), and is now beginning to be used more frequently. With technological advances such as the development of unmanned automatic vehicles (UAVs) (Linchant et al., 2015), the technique has become very popular due to its flexibility, low cost and low risk (e.g. Christiansen et al., 2016, Durban et al., 2016, Dawson et al., 2017, Christiansen et al., 2018).

My finding of inter-annual differences in the body condition of lactating cows in chapter 3 demonstrates that it is possible, using photogrammetric techniques, to build a time series of indicators reflecting humpback whale health and its variability between years. Such a series can provide valuable information about environmental change (e.g. prey availability) in feeding grounds, which can be used to indicate population and potentially ecosystem health. This information can be compared with historical values to investigate variation in a changing climate.

5.10 Recommendations for future research

Marine mammal body condition is known to fluctuate annually in response to environmentally mediated prey availability in feeding grounds (Lockyer, 1986, Ichii et al., 1998). Such relationships have led to marine mammals being considered as sentinels of the ocean and indicators of ecosystem health (Moore, 2008, Bossart, 2011). The concept of using top predators to indicate ecosystem health is not new, with programs such as the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) Environmental Monitoring Program (CEMP) utilising a range of specialist predatory species around the Antarctic continent to 'indicate' the health of the Southern Ocean (SC-CCAMLR, 1985). Currently, seven seabird species and two seal species are used as indicator species in the CEMP (CCAMLR, 2004). The seabirds consist of Adélie, gentoo, chinstrap (*Pygoscelis antarctica*) and macaroni penguins, black-browed albatross, cape petrels (*Daption capense*) and Antarctic petrels (*Thalassoica antarctica*), whilst the seals consist of Antarctic fur seals and crabeater seals (*Lobodon carcinophagus*). As southern hemisphere humpback whales are krill specialists (Kawamura, 1994), annual assessments of their body condition could be used to indicate krill abundance and thus the health of the Southern Ocean. This information could contribute to the CEMP or to marine ecosystem models, which often lack information from top predators (Goedegebuure et al., 2017).

As humpback whales are capital breeders that do not typically feed along their migratory corridor (Chittleborough, 1965), and their cost of travel is low (Brodie, 1975), their body condition in the breeding grounds is closely linked to that in their feeding grounds. For the BSD humpback whales, who feed almost exclusively in the Southern Ocean (Chittleborough, 1965) on Antarctic krill (Kawamura, 1994), body condition assessed in their breeding grounds can be used to indicate ecosystem health in their feeding grounds. In this way, the health of a remote and distant polar ecosystem can be assessed by sampling individuals in easily accessible tropical regions. Furthermore, as humpback whales travel to specific aggregation areas during the breeding season, high numbers of individuals are available for cost-effective sampling (e.g. Nowacek et al., 2011).

Several studies have used a similar approach to link calf production in breeding grounds to environmental conditions in feeding grounds (e.g. Perryman et al., 2002, Leaper et al., 2006). However, calf production can be influenced by failure to ovulate (Rice and Wolman, 1971, Lockyer, 1986) or failure to carry a foetus to term (Perryman et al., 2002), each of which involves different time lags. Body condition is a more direct measure of energy stores that is linked to prey availability in the preceding summer, rather than a delayed response that may relate to conditions several seasons preceding (e.g. Leaper et al., 2006). Male body condition may be the best indicator of conditions in the feeding grounds as it is not influenced by the severe energetic stresses of previous lactation, which may take several years to replenish (e.g. Pettis et al., 2004).

5.11 Conclusion

Through the use of previously forgotten historical whaling records, I have been able to quantify the total energy stores of two large cetaceans with different life histories. This has given us a rare insight into how income and capital breeders, and different reproductive classes of capital breeder, accumulate and allocate energy reserves in

different ways to maximise survival and reproduction. This information is invaluable as data of this detail and extent is not known to be available anywhere else around the globe and is unlikely to be ever collected again. The use of the non-invasive technique of aerial photogrammetry enabled the sampling of free-swimming cetaceans during their annual migration, without the need for capture or close access. By quantifying a decrease in cow body condition and an increase in calf size, over two seasons of lactation, I have established a baseline that can be used to monitor humpback whale condition as the population recovers from commercial whaling. This technique will be invaluable in assessing individual and population health over the coming decades, as the biological effects of climate change unfold. The discovery of calving areas further south than previously recognised illustrates the recovery of the great whales after decimation during the commercial whaling era. The extension of the calving grounds highlights the need for continual monitoring as populations increase and potentially expand into areas of high anthropogenic activity.

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